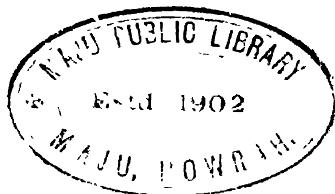


PREFACE.

THE present volume on the Anatomy of Invertebrated Animals fulfils an undertaking to produce a treatise on comparative anatomy for students, into which I entered two-and-twenty years ago. A considerable instalment of the work, relating wholly to the *Invertebrata*, appeared in the 'Medical Times and Gazette' for the years 1856 and 1857, under the title of "Lectures on General Natural History." But a variety of circumstances having conspired, about that time, to compel me to direct my attention more particularly to the *Vertebrata*, I was led to interrupt the publication of the "Lectures" and to complete the Vertebrate half of the proposed work first. This appeared in 1871, as a 'Manual of the Anatomy of Vertebrated Animals.'

A period of incapacity for any serious toil prevented me from attempting, before 1874, to grapple with the immense mass of new and important information respecting the structure, and especially the development, of Invertebrated animals, which the activity of a host of investigators has accumulated of late years.

That my progress has been slow will not surprise any one who is acquainted with the growth of the literature of animal morphology, or with the expenditure of time involved in the attempt to verify for oneself even the cardinal facts of that science; but I have endeavoured, in the last chapter, to supply the most important recent

additions to our knowledge, respecting the groups treated of in those which have long been printed.

When I commenced this work, it was my intention to continue the plan adopted in the 'Manual of the Anatomy of Vertebrated Animals,' of giving a summary account of what appeared to me to be ascertained morphological facts, without referring to my sources of information. I soon found, however, that it would be inconvenient to carry out this scheme consistently; and some of my pages are, I am afraid, somewhat burdened with notes and references.

I am the more careful to mention this circumstance as, had it been my purpose to give any adequate Bibliography, the conspicuous absence of the titles of many important books and memoirs might appear unaccountable and indeed blameworthy.

My object, in writing the book, has been to make it useful to those who wish to become acquainted with the broad outlines of what is at present known of the morphology of the *Invertebrata*; though I have not avoided the incidental mention of facts connected with their physiology and their distribution. On the other hand, I have abstained from discussing questions of ætiology, not because I underestimate their importance, or am insensible to the interest of the great problem of Evolution; but because, to my mind, the growing tendency to mix up ætiological speculations with morphological generalisations will, if unchecked, throw Biology into confusion.

For the student, that which is essential is a knowledge of the facts of morphology; and he should recollect that generalisations are empty formulas, unless there is something in his personal experience which gives reality and substance to the terms of the propositions in which these generalisations are expressed.

The dissection of a single representative of each of the principal divisions of the *Invertebrata* will give the student a more real acquaintance with their comparative anatomy than any amount of reading of this, or any other, book. And I have endeavoured to facilitate practical study by supplying a somewhat full description of individual forms, in the case of the more complicated types.

That the power of repeating a "Classification of Animals," with all the appropriate definitions, has anything to do with genuine knowledge is one of the commonest and most mischievous delusions of both students and their examiners.

The real business of the learner is to gain a true and vivid conception of the characteristics of what may be termed the natural orders of animals. The mode of arrangement, or classification, of these into larger groups is a matter of altogether secondary importance. As such, I have relegated this subject to a subordinate place in the last chapter; and I have thought it unnecessary, either to discuss the systems proposed by others, or to give reasons for passing over, in silence, my own former attempts in this direction.

Of the manifold imperfections in the execution of the task which I have set myself, few will be more sensible than I am; but I trust that the book, such as it is, may be of use to the beginner.

Those who desire to pursue the study of the *Invertebrata* further, will do well to consult the excellent treatises of Von Siebold,* Gegenbaur,† and Claus;‡ and the elaborate

* 'Lehrbuch der vergleichenden Anatomie der wirbellosen Thiere.' 1848. One of the best books on the subject ever written, and still indispensable.

† 'Grundzüge der vergleichenden Anatomie,' 1870; and 'Grundriss der vergleichenden Anatomie,' 1874.

‡ 'Grundzüge der Zoologie.' 3tte Auflage, 1876.

works of Milne-Edwards* and Bronn,† in which a very full Bibliography will be met with. Dr. Rolleston's valuable 'Types of Animal Life,' and the 'Elementary Instruction in Practical Biology,' by myself and Dr. Martin, will prove useful adjuncts to the appliances of the practical worker.

* 'Leçons sur la Physiologie et l'Anatomie comparée de l'homme et des animaux' Tomes I. XII. (incomplete).

† 'Die Klassen und Ordnungen des Thierreichs.' Bde. I.–VI. (incomplete).

London, June, 1877.

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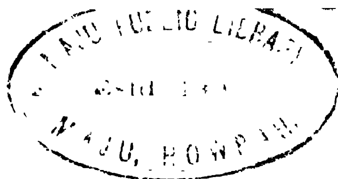


CHAPTER IX.

CHAPTER X.

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CHAPTER XII.



THE ANATOMY

OF

INVERTEBRATED ANIMALS.

INTRODUCTION.

I.—THE GENERAL PRINCIPLES OF BIOLOGY.

THE Biological sciences are those which deal with the phenomena manifested by living matter; and though it is customary and convenient to group apart such of these phenomena as are termed mental, and such of them as are exhibited by men in society, under the heads of Psychology and Sociology, yet it must be allowed that no natural boundary separates the subject matter of the latter sciences from that of Biology. Psychology is inseparably linked with Physiology; and the phases of social life exhibited by animals other than man, which sometimes curiously foreshadow human policy, fall strictly within the province of the biologist.

On the other hand, the biological sciences are sharply marked off from the abiological, or those which treat of the phenomena manifested by not-living matter, in so far as the properties of living matter distinguish it absolutely from all other kinds of things, and as the present state of knowledge furnishes us with no link between the living and the not-living.

These distinctive properties of living matter are—

1. Its *chemical composition*—containing, as it invariably does, one or more forms of a complex compound of carbon, hydrogen, oxygen, and nitrogen, the so-called protein (which has never yet been obtained except as a product of living

bodies) united with a large proportion of water, and forming the chief constituent of a substance which, in its primary unmodified state, is known as *protoplasm*.

2. Its *universal disintegration and waste by oxidation; and its concomitant reintegration by the intus-susception of new matter.*

A process of waste resulting from the decomposition of the molecules of the protoplasm, in virtue of which they break up into more highly oxidated products, which cease to form any part of the living body, is a constant concomitant of life. There is reason to believe that carbonic acid is always one of these waste products, while the others contain the remainder of the carbon, the nitrogen, the hydrogen, and the other elements which may enter into the composition of the protoplasm.

The new matter taken in to make good this constant loss is either a ready-formed protoplasmic material, supplied by some other living being, or it consists of the elements of protoplasm, united together in simpler combinations, which consequently have to be built up into protoplasm by the agency of the living matter itself. In either case, the addition of molecules to those which already existed takes place, not at the surface of the living mass, but by interposition between the existing molecules of the latter. If the processes of disintegration and of reconstruction which characterise life balance one another, the size of the mass of living matter remains stationary, while, if the reconstructive process is the more rapid, the living body *grows*. But the increase of size which constitutes growth is the result of a process of molecular intus-susception, and therefore differs altogether from the process of growth by accretion, which may be observed in crystals and is effected purely by the external addition of new matter—so that, in the well-known aphorism of Linnæus,* the word "grow," as applied to stones, signifies a totally different process from what is called "growth" in plants and animals.

* "*Lapides* crescunt, *vegetabilia* crescunt et vivunt: *animalia* crescunt, vivunt et sentiunt."

3. Its *tendency to undergo cyclical changes*

In the ordinary course of nature, all living matter proceeds from pre-existing living matter, a portion of the latter being detached and acquiring an independent existence. The new form takes on the characters of that from which it arose; exhibits the same power of propagating itself by means of an offshoot; and, sooner or later, like its predecessor, ceases to live, and is resolved into more highly oxidated compounds of its elements.

Thus an individual living body is not only constantly changing its substance, but its size and form are undergoing continual modifications, the end of which is the death and decay of that individual; the continuation of the kind being secured by the detachment of portions which tend to run through the same cycle of forms as the parent. No forms of matter which are either not living, or have not been derived from living matter, exhibit these three properties, nor any approach to the remarkable phenomena defined under the second and third heads. But in addition to these distinctive characters, living matter has some other peculiarities, the chief of which are the dependence of all its activities upon moisture and upon heat, within a limited range of temperature, together with the fact that it usually possesses a certain structure, or organization.

As has been said, a large proportion of water enters into the composition of all living matter, a certain amount of drying arrests vital activity, and the complete abstraction of this water is absolutely incompatible with either actual or potential life. But many of the simpler forms of life may undergo desiccation to such an extent as to arrest their vital manifestations and convert them into the semblance of not-living matter, and yet remain potentially alive, that is to say, on being duly moistened they return to life again. And this revivification may take place after months, or even years, of arrested life.

The properties of living matter are intimately related to temperature. Not only does exposure to heat sufficient to decompose protein matter destroy life, by demolishing the

molecular structure upon which life depends; but all vital activity, all phenomena of nutritive growth, movement, and reproduction are possible only between certain limits of temperature. As the temperature approaches these limits the manifestations of life vanish, though they may be recovered by return to the normal conditions; but if it pass far beyond these limits, death takes place.

This much is clear; but it is not easy to say exactly what the limits of temperature are, as they appear to vary in part with the kind of living matter, and in part with the conditions of moisture which obtain along with the temperature. The conditions of life are so complex in the higher organisms, that the experimental investigation of this question can be satisfactorily attempted only in the lowest and simplest forms. It appears that, in the dry state, these are able to bear far greater extremes both of heat and cold than in the moist condition. Thus Pasteur found that the spores of fungi, when dry, could be exposed without destruction to a temperature of 120°-125° C. (248°-257° Fahr.), while the same spores, when moist, were all killed by exposure to 100° C. (212° Fahr.) On the other hand, Cagniard de la Tour found that dry yeast might be exposed to the extremely low temperature of solid carbonic acid (−60° C. or −76° Fahr.) without being killed. In the moist state he found that it might be frozen and cooled to −5° C. (23° Fahr.), but that it was killed by lower temperatures. However, it is very desirable that these experiments should be repeated, for Cohn's careful observations on *Bacteria* show that, though they fall into a state of torpidity, and, like yeast, lose all their powers of exciting fermentation at, or near, the freezing-point of water, they are not killed by exposure for five hours to a temperature below −10° C. (14° Fahr.) and, for some time, sinking to −18° C. (−0°·4 Fahr.) Specimens of *Spirillum volutans*, which had been cooled to this extent, began to move about some little time after the ice containing them thawed. But Cohn remarks that *Euglenæ*, which were frozen along with them, were all killed and

disorganised, and that the same fate had befallen the higher *Infusoria* and *Rotifera*, with the exception of some encysted *Vorticellæ*, in which the rhythmical movements of the contractile vesicle showed that life was preserved.

Thus it would appear that the resistance of living matter to cold depends greatly on the special form of that matter, and that the limit of the *Euglena*, simple organism as it is, is much higher than that of the *Bacterium*.

Considerations of this kind throw some light upon the apparently anomalous conditions under which many of the lower plants, such as *Protococcus* and the *Diatomaceæ*, and some of the lower animals, such as the *Radiolaria*, are observed to flourish. *Protococcus* has been found, not only on the snows of great heights in temperate latitudes, but covering extensive areas of ice and snow in the Arctic regions, where it must be exposed to extremely low temperatures,—in the latter case for many months together, while the Arctic and Antarctic seas swarm with *Diatomaceæ* and *Radiolaria*. It is on the *Diatomaceæ*, as Hooker has well shown, that all surface life in these regions ultimately depends; and their enormous multitudes prove that their rate of multiplication is adequate to meet the demands made upon them, and is not seriously impeded by the low temperature of the waters, never much above the freezing-point, in which they habitually live.

The maximum limit of heat which living matter can resist is no less variable than its minimum limit. Kuhne found that marine *Amœbæ* were killed when the temperature reached 35° C. (95° Fahr.), while this was not the case with fresh-water *Amœbæ*, which survived a heat of 5°, or even 10°, C. higher. *Actinophrys Eichhornii* was not killed until the temperature rose to 44° or 45° C. *Didymium serpula* is killed at 35° C.; while another *Myxomycete*, *Æthalium septicum*, succumbs only at 40° C.

Cohn (" Untersuchungen uber Bacterien," *Beitrage zur Biologie der Pflanzen*, Heft 2, 1872) has given the results of a series of experiments conducted with the view of ascertaining the temperature at which *Bacteria* are destroyed

when living in a fluid of definite chemical composition, and free from all such complications as must arise from the inequalities of physical condition when solid particles other than the *Bacteria* co-exist with them. The fluid employed contained 0·1 gramme potassium phosphate, 0·1 gr. crystallised magnesium sulphate, 0·1 gr. tribasic calcium phosphate, and 0·2 gr. ammonium tartrate, dissolved in 20 cubic centimetres of distilled water. If to a certain quantity of this "normal fluid" a small proportion of water containing *Bacteria* was added, the multiplication of the *Bacteria* went on with rapidity, whether the mouth of the containing flask was open or hermetically closed. Hermetically-sealed flasks, containing portions of the normal fluid infected with *Bacteria*, were submerged in water heated to various temperatures, the flask being carefully shaken, without being raised out of the water, during its submergence.

The result was, that in those flasks which were thus subjected, for an hour, to a heat of 60°–62° C. (140°–143 Fahr.), the *Bacteria* underwent no development, and the fluid remained perfectly clear. On the other hand, in similar experiments in which the flasks were heated only to 40° or 50° C. (104°–122° Fahr.), the fluid became turbid, in consequence of the multiplication of the *Bacteria*, in the course of from two to three days

I am in the habit of demonstrating annually; that Pasteur's solution and hay infusion, after five minutes' boiling in a flask properly stopped with cotton wool, remain perfectly clear of living organisms, however long they may be kept The same holds good for a solution analogous to Cohn's, but in which all the saline ingredients are ammonia salts ;* and in which *Bacteria* flourish luxuriantly. Prof. Tyndall's large series of experiments give the same results for fluids of the most diverse composition. The cases of milk and some other fluids in which *Bacteria* are said to appear, after

* These were as pure as I could obtain them It is possible the fluid may have contained an infinitesimal proportion of fixed mineral matter.

they have been heated above the boiling-point, require renewed investigation.

Both in Kuhne's and in Cohn's experiments, which last have lately been confirmed and extended by Dr. Roberts of Manchester, it was noted that long exposure to a lower temperature than that which brings about immediate destruction of life, produces the same effect as short exposure to the latter temperature. Thus, though all the *Bacteria* were killed, with certainty, in the normal fluid, by short exposure to temperatures at or above 60° C. (140° Fahr.), Cohn observed that, when a flask containing infected normal fluid was heated to 50°-52° C. (122°-125° Fahr.) for only an hour, the consequent multiplication of the *Bacteria* was manifested much earlier, than in one which had been exposed for two hours to the same temperature.

It appears to be very generally held that the simpler vegetable organisms are deprived of life at temperatures as high as 60° C. (140° Fahr.); but, it is affirmed by competent observers, that *Algæ* have been found living in hot springs at much higher temperatures, namely, from 168° to 208° Fahr., for which latter surprising fact we have the high authority of Descloiseaux. It is no explanation of these phenomena, but only another mode of stating them, to say that these organisms have become "accustomed" to such temperatures. If this degree of heat were absolutely incompatible with the activity of living matter, the plants could no more resist it than they could become "accustomed" to being made red hot. Habit may modify subsidiary, but cannot affect fundamental, conditions.

Recent investigations point to the conclusion that the immediate cause of the arrest of vitality, in the first place, and of its destruction, in the second, is the coagulation of certain substances in the protoplasm, and that the latter contains various coagulable matters, which solidify at different temperatures. And it remains to be seen, how far the death of any form of living matter, at a given temperature, depends on the destruction of its fundamental substance

at that heat, and how far death is brought about by the coagulation of merely accessory compounds.

It may be safely said of all those living things which are large enough to enable us to trust the evidence of microscopes,* that they are heterogeneous optically, and that their different parts, and especially the surface layer, as contrasted with the interior, differ physically and chemically; while, in most living things, mere heterogeneity is exchanged for a definite structure, whereby the body is distinguished into visibly diverse parts, which possess different powers or functions. Living things which present this visible structure are said to be *organised;* and so widely does organisation obtain among living beings, that *organised* and *living* are not unfrequently used as if they were terms of co-extensive applicability. This, however, is not exactly accurate, if it be thereby implied that all living things have a visible organisation, as there are numerous forms of living matter of which it cannot properly be said that they possess either a definite visible structure or permanently specialised organs: though doubtless, the simplest particle of living matter must possess a highly complex molecular structure, which is far beyond the reach of vision.

The broad distinctions which, as a matter of fact, exist between every known form of living substance and every other component of the material world, justify the separation of the biological sciences from all others. But it must not be supposed that the differences between living and not-living matter are such as to bear out the assumption that the forces at work in the one are different from

* In considering the question of the complication of molecular structure which even the smallest and simplest of living beings may possess, it is well to recollect that an organic particle $\frac{1}{10000}$ of an inch in diameter, in which our best microscopes may be incompetent to reveal the slightest differentiation of parts, may be made up of 1,000,000 particles $\frac{1}{1000000}$ of an inch in diameter, while the molecules of matter are probably much less than $\frac{1}{10000000}$ of an inch in diameter. Hence in such a body there is ample scope for any amount of complexity of molecular structure.

those which are to be met with in the other. Considered apart from the phenomena of consciousness, the phenomena of life are all dependent upon the working of the same physical and chemical forces as those which are active in the rest of the world. It may be convenient to use the terms "vitality" and "vital force" to denote the causes of certain great groups of natural operations, as we employ the names of "electricity" and "electrical force" to denote others; but it ceases to be proper to do so, if such a name implies the absurd assumption that either "electricity" or "vitality" are entities playing the part of efficient causes of electrical or vital phenomena. A mass of living protoplasm is simply a molecular machine of great complexity, the total results of the working of which, or its vital phenomena, depend, on the one hand, upon its construction, and, on the other, upon the energy supplied to it; and to speak of "vitality" as anything but the name of a series of operations is as if one should talk of the "horologity" of a clock.

Living matter, or protoplasm and the products of its metamorphosis, may be regarded under four aspects —

(1.) It has a certain external and internal form, the latter being more usually called structure;

(2.) It occupies a certain position in space and in time;

(3.) It is the subject of the operation of certain forces, in virtue of which it undergoes internal changes, modifies external objects, and is modified by them; and

(4.) Its form, place, and powers are the effects of certain causes.

In correspondence with these four aspects of its subject, Biology is divisible into four chief subdivisions—I. MORPHOLOGY; II. DISTRIBUTION; III. PHYSIOLOGY; IV. ÆTIOLOGY.

I. MORPHOLOGY.

So far as living beings have a form and structure, they fall within the province of *Anatomy* and *Histology*, the latter being merely a name for that ultimate optical analysis

of living structure which can be carried out only by the aid of the microscope.

And, in so far as the form and structure of any living being are not constant during the whole of its existence, but undergo a series of changes from the commencement of that existence to its end, living beings have a *Development*. The history of development is an account of the anatomy of a living being at the successive periods of its existence, and of the manner in which one anatomical stage passes into the next.

Finally, the systematic statement and generalisation of the facts of Morphology, in such a manner as to arrange living beings in groups, according to their degrees of likeness, is *Taxonomy*.

The study of Anatomy and Development has brought to light certain generalisations of wide applicability and great importance.

1. It has been said that the great majority of living beings present a very definite structure. Unassisted vision and ordinary dissection suffice to separate the body of any of the higher animals, or plants, into fabrics of different sorts, which always present the same general arrangement in the same organism, but are combined in different ways in different organisms. The discrimination of these comparatively few fabrics, or *tissues*, of which organisms are composed, was the first step towards that ultimate analysis of visible structure which has become possible only by the recent perfection of microscopes and of methods of preparation.

Histology, which embodies the results of this analysis, shows that every tissue of a plant is composed of more or less modified structural elements, each of which is termed a *cell*; which cell, in its simplest condition, is merely a spheroidal mass of protoplasm, surrounded by a coat or sac —the *cell-wall*—which contains cellulose. In the various tissues, these cells may undergo innumerable modifications of form—the protoplasm may become differentiated into a nucleus with its nucleolus, a primordial utricle, and a

cavity filled with a watery fluid, and the cell-wall may be variously altered in composition or in structure, or may coalesce with others. But, however extensive these changes may be, the fact that the tissues are made up of morphologically distinct units—the cells—remains patent. And, if any doubt could exist on the subject, it would be removed by the study of development, which proves that every plant commences its existence as a simple cell, identical in its fundamental characters with the less modified of those cells of which the whole body is composed.

But it is not necessary to the morphological unit of the plant that it should be always provided with a cell-wall Certain plants, such as *Protococcus*, spend longer or shorter periods of their existence in the condition of a mere spheroid of protoplasm, devoid of any cellulose wall, while, at other times, the protoplasmic body becomes enclosed within a cell-wall, fabricated by its superficial layer.

Therefore, just as the nucleus, the primordial utricle, and the central fluid are no essential constituents of the morphological unit of the plant, but represent results of its metamorphosis, so the cell-wall is equally unessential; and either the term "cell" must acquire a merely technical significance as the equivalent of morphological unit, or some new term must be invented to describe the latter. On the whole, it is probably least inconvenient to modify the sense of the word "cell."

The histological analysis of animal tissues has led to similar results and to difficulties of terminology of precisely the same character. In the higher animals, however, the modifications which the cells undergo are so extensive, that the fact that the tissues are, as in plants, resolvable into an aggregation of morphological units, could never have been established without the aid of the study of development, which proves that the animal, no less than the plant, commences its existence as a simple cell, fundamentally identical with the less modified cells which are found in the tissues of the adult.

Though the nucleus is very constant among animal cells,

it is not universally present; and among the lowest forms of animal life, the protoplasmic mass which represents the morphological unit may be, as in the lowest plants, devoid of a nucleus. In the animal, the cell-wall never has the character of a shut sac containing cellulose; and it is not a little difficult, in many cases, to say how much of the so-called "cell-wall" of the animal cell answers to the "primordial utricle" and how much to the proper "cellulose cell-wall" of the vegetable cell. But it is certain that in the animal, as in the plant, neither cell-wall nor nucleus are essential constituents of the cell, inasmuch as bodies which are unquestionably the equivalents of cells—true morphological units—may be mere masses of protoplasm, devoid alike of cell-wall and nucleus.

For the whole living world, then, it results:—that the morphological unit—the primary and fundamental form of life—is merely an individual mass of protoplasm, in which no further structure is discernible; that independent living forms may present but little advance on this structure; and that all the higher forms of life are aggregates of such morphological units or cells, variously modified.

Moreover, all that is at present known tends to the conclusion, that, in the complex aggregates of such units of which all the higher animals and plants consist, no cell has arisen otherwise than by becoming separated from the protoplasm of a pre-existing cell; whence the aphorism "*Omnis cellula e cellulâ.*"

It may further be added, as a general truth applicable to nucleated cells, that the nucleus rarely undergoes any considerable modification, the structures characteristic of the tissues being formed at the expense of the more superficial protoplasm of the cells; and that, when nucleated cells divide, the division of the nucleus, as a rule, precedes that of the whole cell.

2. In the course of its development every cell proceeds from a condition in which it closely resembles every other cell, through a series of stages of gradually increasing divergence, until it reaches that condition in which it

presents the characteristic features of the elements of a special tissue. The development of the cell is therefore a gradual progress from the general to the special state.

The like holds good of the development of the body as a whole. However complicated one of the higher animals or plants may be, it begins its separate existence under the form of a nucleated cell. This, by division, becomes converted into an aggregate of nucleated cells· the parts of this aggregate, following different laws of growth and multiplication, give rise to the rudiments of the organs; and the parts of these rudiments again take on those modes of growth multiplication and metamorphosis which are needful to convert the rudiment into the perfect structure.

The development of the organism as a whole, therefore, repeats in principle the development of the cell. It is a progress from a general to a special form, resulting from the gradual differentiation of the primitively similar morphological units of which the body is composed.

Moreover, when the stages of development of two animals are compared, the number of these stages which are similar to one another is, as a general rule, proportional to the closeness of the resemblance of the adult forms; whence it follows that the more closely any two animals are allied in adult structure, the later are their embryonic conditions distinguishable. And this general rule holds for plants no less than for animals.

The broad principle, that the form in which the more complex living things commence their development is always the same, was first expressed by Harvey in his famous aphorism "*Omne vivum ex ovo*," which was intended simply as a morphological generalisation, and in no wise implied the rejection of spontaneous generation, as it is commonly supposed to do. Moreover, Harvey's study of the development of the chick led him to promulgate that theory of "epigenesis," in which the doctrine that development is a progress from the general to the special is implicitly contained.

Caspar F. Wolff furnished further. and indeed conclu-

sive proof of the truth of the theory of epigenesis: but, unfortunately, the authority of Haller and the speculations of Bonnet led science astray, and it was reserved for Von Baer to put the nature of the process of development in its true light, and to formulate it in his famous law.

3. Development, then, is a process of differentiation by which the primitively similar parts of the living body become more and more unlike one another.

This process of differentiation may be effected in several ways.

(1.) The protoplasm of the germ may not undergo division and conversion into a cell aggregate; but various parts of its outer and inner substance may be metamorphosed directly into those physically and chemically different materials which constitute the body of the adult. This occurs in such animals as the *Infusoria*, and in such plants as the unicellular *Algæ* and *Fungi*

(2.) The germ may undergo division, and be converted into an aggregate of *division masses*, or *blastomeres*, which become cells and give rise to the tissues by undergoing a metamorphosis of the same kind as that to which the whole body is subjected in the preceding case.

The body, formed in either of these ways, may, as a whole, undergo metamorphosis by differentiation of its parts; and this differentiation may take place without reference to any axis of symmetry, or it may have reference to such an axis. In the latter case, the parts of the body which become distinguishable may correspond on the two sides of the axis (bilateral symmetry), or may correspond along several lines parallel with the axis (radial symmetry).

The bilateral or radial symmetry of the body may be further complicated by its segmentation, or separation by divisions transverse to the axis, into parts, each of which corresponds with its predecessor or successor in the series.

In the segmented body, the segments may or may not give rise to symmetrically or asymmetrically disposed processes, which are *appendages*, using that word in its most general sense.

And the highest degree of complication of structure, in both animals and plants, is attained by the body when it becomes divided into segments provided with appendages; when the segments not only become very different from one another, but some coalesce and lose their primitive distinctness; and when the appendages and the segments into which they are subdivided similarly become differentiated and coalesce.

It is in virtue of such processes that the flowers of plants, and the heads and limbs of the *Arthropoda* and of the *Vertebrata*, among animals, attain their extraordinary diversity and complication of structure. A flower-bud is a segmented body or axis, with a certain number of whorls of appendages; and the perfect flower is the result of the gradual differentiation and confluence of these primitively similar segments and their appendages. The head of an insect or of a crustacean is, in like manner, composed of a number of segments, each with its pair of appendages, which by differentiation and confluence are converted into the feelers and variously modified oral appendages of the adult.

In some complex organisms, the process of differentiation, by which they pass from the condition of aggregated embryo cells to the adult, can be traced back to the laws of growth of the two or more cells into which the embryo cell is divided, each of these cells giving rise to a particular portion of the adult organism. Thus the fertilised embryo cell in the archegonium of a fern divides into four cells, one of which gives rise to the rhizome of the young fern, another to its first rootlet, while the other two are converted into a placenta-like mass which remains imbedded in the prothallus.

The structure of the stem of *Chara* depends upon the different properties of the cells, which are successively derived by transverse division from the apical cell. An *inter-nodal* cell, which elongates greatly, and does not divide, is succeeded by a *nodal* cell, which elongates but little, and becomes greatly subdivided; this by another

inter-nodal cell, and so on in regular alternation. In the same way the structure of the stem, in all the higher plants, depends upon the laws which govern the manner of division and of metamorphosis of the apical cells, and of their continuation in the *cambium* layer.

In all animals which consist of cell-aggregates, the cells of which the embryo is at first composed arrange themselves by the splitting, or by a process of invagination, of the blastoderm into two layers, the *epiblast* and the *hypoblast*, between which a third intermediate layer, the *mesoblast*, appears; and each layer gives rise to a definite group of organs in the adult. Thus, in the *Vertebrata*, the epiblast gives rise to the cerebro-spinal axis, and to the epidermis and its derivatives, the hypoblast, to the epithelium of the alimentary canal and its derivatives, and the mesoblast, to intermediate structures. The tendency of recent inquiry is to prove that the several layers of the germ evolve analogous organs in invertebrate animals, and to indicate the possibility of tracing the several germ layers back to the blastomeres of the yelk, from the subdivision of which they proceed.

It is conceivable that all the forms of life should have presented about the same differentiation of structure, and should have differed from one another by superficial characters, each form passing by insensible gradations into those most like it. In this case Taxonomy, or the classification of morphological facts, would have had to confine itself to the formation of a serial arrangement, representing the serial gradation of these forms in nature.

It is conceivable, again, that living beings should have differed as widely in structure as they actually do, but that the interval between any two extreme forms should have been filled up by an unbroken series of gradations; in which case, again, classification could only effect the formation of series—the strict definition of groups would be as impossible as in the former case.

As a matter of fact, living beings differ enormously, not

only in differentiation of structure, but in the modes in which that differentiation is brought about; and the intervals between extreme forms are not filled up, in the existing world, by complete series of gradations. Hence it arises that living beings are, to a great extent, susceptible of classification into groups, the members of each group resembling one another, and differing from all the rest, by certain definite peculiarities.

No two living beings are exactly alike, but it is a matter of observation that, among the endless diversities of living things, some constantly resemble one another so closely that it is impossible to draw any line of demarcation between them, while they differ only in such characters as are associated with sex. Such as thus closely resemble one another constitute a *morphological species*; while different morphological species are defined by constant characters which are not merely sexual.

The comparison of these lowest groups, or morphological species, with one another, shows that more or fewer of them possess some character or characters in common—some feature in which they resemble one another and differ from all other species—and the group or higher order thus formed is a *genus*. The generic groups thus constituted are susceptible of being arranged in a similar manner into groups of successively higher order, which are known as *families*, *orders*, *classes*, and the like.

The method pursued in the classification of living forms is, in fact, exactly the same as that followed by the maker of an index in working out the heads indexed. In an alphabetical arrangement, the classification may be truly termed a morphological one, the object being to put into close relation all those leading words which resemble one another in the arrangement of their letters, that is, in their form, and to keep apart those which differ in structure. Headings which begin with the same word, but differ otherwise, might be compared to genera with their species; the groups of words with the same first two syllables to families; those with identical first syllables to orders; and

those with the same initial letter to classes. But there is this difference between the index and the Taxonomic arrangement of living forms, that in the former there is nothing but an arbitrary relation between the various classes, while, in the latter, the classes are similarly capable of co-ordination into larger and larger groups, until all are comprehended under the common definition of living beings.

The differences between "artificial" and "natural" classifications are differences in degree, and not in kind. In each case the classification depends upon likeness; but in an artificial classification some prominent and easily observed feature is taken as the mark of resemblance or dissemblance; while, in a natural classification, the things classified are arranged according to the totality of their morphological resemblances, and the features which are taken as the marks of groups are those which have been ascertained by observation to be the indications of many likenesses or unlikenesses. And thus a natural classification is a great deal more than a mere index. It is a statement of the marks of similarity of organisation; of the kinds of structure which, as a matter of experience, are found universally associated together; and, as such, it furnishes the whole foundation for those indications by which conclusions as to the nature of the whole of an animal are drawn from a knowledge of some part of it.

When a palæontologist argues from the characters of a bone or of a shell to the nature of the animal to which that bone or shell belonged, he is guided by the empirical morphological laws established by wide observation, that such a kind of bone or shell is associated with such and such structural features in the rest of the body, and no others. And it is these empirical laws which are embodied and expressed in a natural classification.

II. Distribution.

Living beings occupy certain portions of the surface of the earth, inhabiting either the dry land, or the fresh or salt waters; or being competent to maintain their existence in either.* In any given locality, it is found that these different media are inhabited by different kinds of living beings; and that the same medium, at different heights in the air and at different depths in the water, has different living inhabitants.

Moreover, the living populations of localities which differ considerably in latitude, and hence in climate, always present considerable differences. But the converse proposition is not true; that is to say, localities which differ in longitude, even if they resemble one another in climate, often have very dissimilar *Faunæ* and *Floræ*.

It has been discovered by careful comparison of local Faunæ and Floræ, that certain areas of the earth's surface are inhabited by groups of animals and plants which are not found elsewhere, and which thus characterize each of these areas. Such areas are termed *Provinces of Distribution*. There is no parity between these provinces in extent, nor in the physical configuration of their boundaries, and, in reference to existing conditions, nothing can appear to be more arbitrary and capricious than the distribution of living beings.

The study of distribution is not confined to the present order of nature; but, by the help of geology, the naturalist is enabled to obtain clear, though too fragmentary, evidence of the characters of the faunæ and floræ of antecedent epochs. The remains of organisms which are contained in the stratified rocks prove that, in any given part of the earth's surface, the living population of earlier epochs was different from that which now exists in the locality; and that, on the whole, the difference becomes greater the farther we go back in time. The organic remains which are found in the later Cainozoic deposits of any district

are always closely allied to those now found in the province of distribution in which that locality is included; while in the older Cainozoic the resemblance is less; and in the Mesozoic, and the Palæozoic strata, the fossils may be similar to creatures at present living in some other province, or may be altogether unlike any which now exist.

In any given locality, the succession of living forms may appear to be interrupted by numerous breaks—the associated species in each fossiliferous bed being quite distinct from those above and those below them. But the tendency of all palæontological investigation is to show that these breaks are only apparent, and arise from the incompleteness of the series of remains which happens to have been preserved in any given locality. As the area over which accurate geological investigations have been carried on extends, and as the fossiliferous rocks found in one locality fill up the gaps left in another, so do the abrupt demarcations between the faunæ and floræ of successive epochs disappear—a certain proportion of the genera and even of the species of every period, great or small, being found to be continued for a longer or shorter time into the next succeeding period. It is evident, in fact, that the changes in the living population of the globe which have taken place during its history, have been effected, not by the sudden replacement of one set of living beings by another, but by a process of slow and gradual introduction of new species, accompanied by the extinction of the older forms.

It is a remarkable circumstance, that, in all parts of the globe in which fossiliferous rocks have yet been examined, the successive terms of the series of living forms which have thus succeeded one another are analogous. The life of the Mesozoic epoch is everywhere characterised by the abundance of some groups of species of which no trace is to be found in either earlier or later formations; and the like is true of the Palæozoic epoch. Hence it follows, not only that there has been a succession of species, but that the general nature of that succession has been the same all

over the globe; and it is on this ground that fossils are so important to the geologist as marks of the relative age of rocks.

The determination of the morphological relations of the species which have thus succeeded one another is a problem of profound importance and difficulty, the solution of which, however, is already clearly indicated. For, in several cases, it is possible to show that, in the same geographical area, a form A, which existed during a certain geological epoch, has been replaced by another form B, at a later period, and that this form B has been replaced, still later, by a third form C. When these forms, A, B, and C, are compared together they are found to be organized upon the same plan, and to be very similar even in most of the details of their structure; but B differs from A by a slight modification of some of its parts, which modification is carried to a still greater extent in C.

In other words, A, B, and C differ from one another in the same fashion as the earlier and later stages of the embryo of the same animals differ; and, in successive epochs, we have the group presenting that progressive specialisation which characterises the development of the individual. Clear evidence that this progressive specialisation of structure has actually occurred has as yet been obtained in only a few cases (*e.g.*, *Equidæ*, *Crocodilia*), and these are confined to the highest and most complicated forms of life; while it is demonstrable that, even as reckoned by geological time, the process must have been exceedingly slow.

Among the lower and less complicated forms, the evidence of progressive modification, furnished by comparison of the oldest with the latest forms, is slight, or absent; and some of these have certainly persisted, with very little change, from extremely ancient times to the present day. It is as important to recognise the fact that certain forms of life have thus persisted, as it is to admit that others have undergone progressive modification.

It has been said that the successive terms in the series

of living forms are analogous in all parts of the globe. But the species which constitute the corresponding or *homotaxic* terms in the series, in different localities, are not identical. And, though the imperfection of our knowledge at present precludes positive assertion, there is every reason to believe that geographical provinces have existed throughout the period during which organic remains furnish us with evidence of the existence of life. The wide distribution of certain Palæozoic forms does not militate against this view; for the recent investigations into the nature of the deep-sea fauna have shown that numerous *Crustacea*, *Echinodermata*, and other invertebrate animals, have as wide a distribution now as their analogues possessed in the Silurian epoch.

III. Physiology.

Thus far, living beings have been regarded merely as definite forms of matter, and Biology has presented no considerations of a different order from those which meet the student of Mineralogy. But living things are not only natural bodies, having a definite form and mode of structure, growth, and development. They are machines in action; and, under this aspect, the phenomena which they present have no parallel in the mineral world.

The actions of living matter are termed its *functions*; and these functions, varied as they are, may be reduced to three categories. They are either—(1), functions which affect the material composition of the body, and determine its mass, which is the balance of the processes of waste on the one hand and those of assimilation on the other. Or (2), they are functions which subserve the process of reproduction, which is essentially the detachment of a part endowed with the power of developing into an independent whole. Or (3), they are functions in virtue of which one part of the body is able to exert a direct influence on another, and the body, by its parts or as a whole, becomes a source of molar motion. The first may be termed *susten-*

tative, the second *generative*, and the third *correlative* functions.

Of these three classes of functions the first two only can be said to be invariably present in living beings, all of which are nourished, grow, and multiply. But there are some forms of life, such as many *Fungi*, which are not known to possess any powers of changing their form; in which the protoplasm exhibits no movements, and reacts upon no stimulus; and in which any influence which the different parts of the body exert upon one another must be transmitted indirectly from molecule to molecule of the common mass. In most of the lowest plants, however, and in all animals yet known, the body either constantly or temporarily changes its form, either with or without the application of a special stimulus, and thereby modifies the relations of its parts to one another, and of the whole to surrounding bodies; while, in all the higher animals, the different parts of the body are able to affect, and be affected by, one another, by means of a special tissue, termed *nerve*. Molar motion is effected on a large scale by means of another special tissue, *muscle*; and the organism is brought into relation with surrounding bodies by means of a third kind of special tissue—that of the *sensory organs*—by means of which the forces exerted by surrounding bodies are transmuted into affections of nerve.

In the lowest forms of life, the functions which have been enumerated are seen in their simplest forms, and they are exerted indifferently, or nearly so, by all parts of the protoplasmic body; and the like is true of the functions of the body of even the highest organisms, so long as they are in the condition of the nucleated cell, which constitutes the starting-point of their development. But the first process in that development is the division of the germ into a number of morphological units or blastomeres, which, eventually, give rise to cells; and as each of these possesses the same physiological functions as the germ itself, it follows that each morphological unit is also a physiological unit, and the multicellular mass is strictly a com-

pound organism, made up of a multitude of physiologically independent cells. The physiological activities manifested by the complex whole represent the sum, or rather the resultant, of the separate and independent physiological activities resident in each of the simpler constituents of that whole.

The morphological changes which the cells undergo in the course of the further development of the organism, do not affect their individuality; and, notwithstanding the modification and confluence of its constituent cells, the adult organism, however complex, is still an aggregate of morphological units. Nor is it less an aggregate of physiological units, each of which retains its fundamental independence, though that independence becomes restricted in various ways.

Each cell, or that element of a tissue which proceeds from the modification of a cell, must needs retain its sustentative functions so long as it grows or maintains a condition of equilibrium; but the most completely metamorphosed cells show no trace of the generative function, and many exhibit no correlative functions. Contrariwise those cells of the adult organism which are the unmetamorphosed derivatives of the germ, exhibit all the primary functions, not only nourishing themselves and growing, but multiplying, and frequently showing more or less marked movements.

Organs are parts of the body which perform particular functions. In strictness, perhaps, it is not quite right to speak of organs of sustentation or generation, each of these functions being necessarily performed by the morphological unit which is nourished or reproduced. What are called the organs of these functions are the apparatuses by which certain operations, subsidiary to sustentation and generation, are carried on.

Thus, in the case of the sustentative functions, all those organs may be said to contribute to these functions which are concerned in bringing nutriment within the reach of the ultimate cells, or in removing waste matter from them;

while in the case of the generative function, all those organs contribute to the function which produce the cells from which germs are given off; or help in the evacuation, or fertilisation, or development of these germs.

On the other hand, the correlative functions, so long as they are exerted by a simple undifferentiated morphological unit or cell, are of the simplest character, consisting of those modifications of position which can be effected by mere changes in the form or arrangement of the parts of the protoplasm, or of those prolongations of the protoplasm which are called pseudopodia or cilia. But, in the higher animals and plants, the movements of the organism and of its parts are brought about by the change of the form of certain tissues, the property of which is to shorten in one direction when exposed to certain stimuli. Such tissues are termed *contractile*; and, in their most fully developed condition, *muscular*. The stimulus by which this contraction is naturally brought about is a molecular change, either in the substance of the contractile tissue itself, or in some other part of the body; in which latter case, the motion which is set up in that part of the body must be propagated to the contractile tissue through the intermediate substance of the body. In plants, there seems to be no question that parts which retain a hardly modified cellular structure may serve as channels for the transmission of this molecular motion; whether the same is true of animals is not certain. But, in all the more complex animals, a peculiar fibrous tissue—*nerve*—serves as the agent by which contractile tissue is affected by changes occurring elsewhere, and by which contractions thus initiated are co-ordinated and brought into harmonious combination. While the sustentative functions in the higher forms of life are still, as in the lower, fundamentally dependent upon the powers inherent in all the physiological units which make up the body, the correlative functions are, in the former, deputed to two sets of specially modified units, which constitute the muscular and the nervous tissues.

When the different forms of life are compared together

as physiological machines, they are found to differ as machines of human construction do. In the lower forms, the mechanism, though perfectly well adapted to do the work for which it is required, is rough, simple, and weak; while, in the higher, it is finished, complicated, and powerful. Considered as machines, there is the same sort of difference between a polype and a horse as there is between a distaff and a spinning-jenny. In the progress from the lower to the higher organism, there is a gradual differentiation of organs and of functions. Each function is separated into many parts, which are severally entrusted to distinct organs. To use the striking phrase of Milne-Edwards, in passing from low to high organisms, there is a division of physiological labour. And exactly the same process is observable in the development of any of the higher organisms; so that, physiologically as well as morphologically, development is a progress from the general to the special.

Thus far, the physiological activities of living matter have been considered in themselves, and without reference to anything that may affect them in the world outside the living body. But living matter acts on, and is powerfully affected by, the bodies which surround it; and the study of the influence of the "conditions of existence" thus determined constitutes a most important part of Physiology.

The sustentative functions, for example, can only be exerted under certain conditions of temperature, pressure, and light, in certain media, and with supplies of particular kinds of nutritive matter; the sufficiency of which supplies, again, is greatly influenced by the competition of other organisms, which, striving to satisfy the same needs, give rise to the passive "struggle for existence." The exercise of the correlative functions is influenced by similar conditions, and by the direct conflict with other organisms, which constitutes the active struggle for existence. And, finally, the generative functions are subject to extensive modifications, dependent partly upon what are commonly called external conditions, and partly upon wholly unknown agencies.

In the lowest forms of life, the only mode of generation at present known is the division of the body into two or more parts, each of which then grows to the size and assumes the form of its parent, and repeats the process of multiplication. This method of multiplication by *fission* is properly called generation, because the parts which are separated are severally competent to give rise to individual organisms of the same nature as that from which they arose.

In many of the lowest organisms the process is modified so far that, instead of the parent dividing into two equal parts, only a small portion of its substance is detached, as a bud, which developes into the likeness of its parent. This is generation by *gemmation*. Generation by fission and by gemmation are not confined to the simplest forms of life, however. On the contrary, both modes of multiplication are common not only among plants, but among animals of considerable complexity.

The multiplication of flowering plants by bulbs, that of annelids by fission, and that of polypes by budding, are well-known examples of these modes of reproduction. In all these cases, the bud or the segment consists of a multitude of more less metamorphosed cells. But, in other instances, a single cell detached from a mass of such undifferentiated cells contained in the parental organism is the foundation of the new organism, and it is hard to say whether such a detached cell may be more fitly called a bud or a segment—whether the process is more akin to fission or to gemmation.

In all these cases the development of the new being from the detached germ takes place without the influence of other living matter. Common as the process is in plants and in the lower animals, it becomes rare among the higher animals. In these, the reproduction of the whole organism from a part, in the way indicated above, ceases. At most we find that the cells at the end of an amputated portion of the organism are capable of reproducing the lost part; in the very highest animals, even this power

vanishes in the adult; and, in most parts of the body, though the undifferentiated cells are capable of multiplication, their progeny grow, not into whole organisms like that of which they form a part, but into elements of the tissues.

Throughout almost the whole series of living beings, however, we find concurrently with the process of *agamogenesis*, or asexual generation, another method of generation, in which the development of the germ into an organism resembling the parent depends on an influence exerted by living matter different from the germ. This is *gamogenesis* or sexual generation. Looking at the facts broadly, and without reference to many exceptions in detail, it may be said that there is an inverse relation between agamogenetic and gamogenetic reproduction. In the lowest organisms gamogenesis has not yet been observed, while in the highest agamogenesis is absent. In many of the lower forms of life agamogenesis is the common and predominant mode of reproduction, while gamogenesis is exceptional; on the contrary, in many of the higher, while gamogenesis is the rule, agamogenesis takes place exceptionally.

In its simplest condition, which is termed "*conjugation*," sexual generation consists in the coalescence of two similar masses of protoplasmic matter, derived from different parts of the same organism, or from two organisms of the same species, and the single mass which results from the fusion develops into a new organism.

In the majority of cases, however, there is a marked morphological difference between the two factors in the process, and then one is called the *male*, and the other the *female* element. The female element is relatively large, and undergoes but little change of form. In all the higher plants and animals it is a nucleated cell, to which a greater or less amount of nutritive material, constituting a *food-yelk*, may be added.

The male element, on the other hand, is relatively small. It may be conveyed to the female element by an outgrowth of the wall of its cell, which is short in many

Algæ and *Fungi*, but becomes an immensely elongated tubular filament, in the case of the pollen cell of flowering plants. But, more commonly, the protoplasm of the male cell becomes converted into rods or filaments, which usually are in active vibratile movement, and sometimes are propelled by numerous cilia. Occasionally, however, as in many *Nematoidea* and *Arthropoda*, they are devoid of mobility.

The manner in which the contents of the pollen tube affect the embryo cell in flowering plants is unknown, as no perforation through which the contents of the pollen tube may pass, so as actually to mix with the substance of the embryo cell, have been discovered; and there is the same difficulty with respect to the conjugative processes of some of the *Cryptogamia*. But in the great majority of plants, and in all animals, there can be no doubt that the substance of the male element actually mixes with that of the female, so that, in all these cases, the sexual process remains one of conjugation; and impregnation is the physical admixture of protoplasmic matter derived from two sources, which may be either different parts of the same organism, or different organisms.

The effect of impregnation appears in all cases to be that the impregnated protoplasm tends to divide into portions (*blastomeres*), which may remain united as a single cell-aggregate, or some or all of which may become separate organisms. A longer or shorter period of rest, in many cases, intervenes between the act of impregnation and the commencement of the process of division.

As a general rule, the female cell which directly receives the influence of the male is that which undergoes division and eventual development into independent germs; but there are some plants, such as the *Florideæ*, in which this is not the case. In these, the protoplasmic body of the trichogyne, which unites with the spermatozooids, does not undergo division itself, but transmits some influence to adjacent cells, in virtue of which they become subdivided into independent germs or spores.

There is still much obscurity respecting the reproductive processes of the *Infusoria*; but, in the *Vorticellidæ*, it would appear that conjugation merely determines a condition of the whole organism, which gives rise to the division of the endoplast or so-called nucleus, by which germs are thrown off; and if this be the case, the process would have some analogy to what takes place in the *Florideæ*.

On the other hand, the process of conjugation by which two distinct *Diporpæ* combine into that extraordinary double organism, the *Diplozoon paradoxum*, does not directly give rise to germs, but determines the development of the sexual organs in each of the conjugated individuals; and the same process takes place in a large number of the *Infusoria*, if what are supposed to be male sexual elements in them are really such.

The process of impregnation in the *Florideæ* is remarkably interesting, from its bearing upon the changes which fecundation is known to produce upon parts of the parental organism other than the ovum, even in the highest animals and plants.

The nature of the influence exerted by the male element upon the female is wholly unknown. No morphological distinction can be drawn between those cells which are capable of reproducing the whole organism without impregnation, and those which need it, as is obvious from what happens in insects, where eggs which ordinarily require impregnation, exceptionally, as in many moths, or regularly, as in the case of the drones among bees, develop without impregnation. Even in the higher animals, such as the fowl, the earlier stages of division of the germ may take place without impregnation.

In fact, generation may be regarded as a particular case of cell multiplication, and impregnation simply as one of the many conditions which may determine or affect that process. In the lowest organisms, the simple protoplasmic mass divides, and each part retains all the physiological properties of the whole, and consequently constitutes a germ whence the whole body can be reproduced. In more ad-

vanced organisms, each of the multitude of cells into which the embryo cell is converted at first, probably retains all, or nearly all, the physiological capabilities of the whole, and is capable of serving as a reproductive germ; but as division goes on, and many of the cells which result from division acquire special morphological and physiological properties, it seems not improbable that they, in proportion, lose their more general characters. In proportion, for example, as the tendency of a given cell to become a muscle cell or a cartilage cell is more marked and definite, it is readily conceivable that its primitive capacity to reproduce the whole organism should be reduced, though it might not be altogether abolished. If this view is well based, the power of reproducing the whole organism would be limited to those cells which had acquired no special tendencies, and consequently had retained all the powers of the primitive cell in which the organism commenced its existence. The more extensively diffused such cells were, the more generally might multiplication by budding or fission take place; the more localised, the more limited would be the parts of the organism in which such a process would take place. And even where such cells occurred, their development or non-development might be connected with conditions of nutrition. It depends on the nutriment supplied to the female larva of a bee whether it shall become a neuter or a sexually perfect female; and the sexual perfection of a large proportion of the internal parasites is similarly dependent upon their food, and perhaps on other conditions, such as the temperature of the medium in which they live. Thus the gradual disappearance of agamogenesis in the higher animals would be related with that increasing specialisation of function which is their essential characteristic; and when it ceases to occur altogether, it may be supposed that no cells are left which retain unmodified the powers of the primitive embryo cell. The organism is like a society in which every one is so engrossed by his special business that he has neither time nor inclination to marry.

Even the female elements in the highest organisms,

little as they differ to all appearance from undifferentiated cells, and though they are directly derived from epithelial cells which have undergone very little modification from the condition of blastomeres, are incapable of full development unless they are subjected to the influence of the male element, which may, as Caspar Wolff suggested, be compared to a kind of nutriment. But it is a living nutriment, in some respects comparable to that which would be supplied to an animal kept alive by transfusion, and its molecules transfer to the impregnated embryo cell all the special characters of the organism to which it belonged.

The tendency of the germ to reproduce the characters of its immediate parents, combined, in the case of sexual generation, with the tendency to reproduce the characters of the male, is the source of the singular phenomena of hereditary transmission. No structural modification is so slight, and no functional peculiarity is so insignificant in either parent that it may not make its appearance in the offspring. But the transmission of parental peculiarities depends greatly upon the manner in which they have been acquired. Such as have arisen naturally, and have been hereditary through many antecedent generations, tend to appear in the progeny with great force; while artificial modifications, such for example, as result from mutilation, are rarely if ever, transmitted. Circumcision through innumerable ancestral generations does not appear to have reduced that rite to a mere formality, as it should have done, if the abbreviated prepuce had become hereditary in the descendants of Abraham; while modern lambs are born with long tails, notwithstanding the long-continued practice of cutting those of every generation short. And it remains to be seen whether the supposed hereditary transmission of the habit of retrieving among dogs is really what it seems at first sight to be; on the other side, Brown-Séquard's case of the transmission of artificially induced epilepsy in guinea-pigs is undoubtedly very weighty.

Although the germ always tends to reproduce, directly or indirectly, the organism from which it is derived, the

result of its development differs somewhat from the parent. Usually the amount of variation is insignificant, but it may be considerable, as in the so-called "sports," and such variations, whether useful or useless, may be transmitted with great tenacity to the offspring of the subjects of them.

In many plants and animals which multiply both asexually and sexually, there is no definite relation between the agamogenetic and the gamogenetic phenomena. The organism may multiply asexually before, or after, or concurrently with, the occurrence of sexual generation.

But in a great many of the lower organisms, both animal and vegetable, the organism (A) which results from the impregnated germ produces offspring only agamogenetically. It thus gives rise to a series of independent organisms, (B. B. B, . . .), which are more or less different from A, and which sooner or later acquire generative organs. From their impregnated germs A is reproduced. The process thus described is what has been termed the "alternation of generations" under its simplest form,—for example, as it is exhibited by the *Salpæ*. In more complicated cases, the independent organisms which correspond with B may give rise agamogenetically to others (B_1), and these to others (B_2), and so on (*e.g. Aphis*). But, however long the series, a final term appears which developes sexual organs, and reproduces A. The "alternation of generations" is, therefore, in strictness, an alternation of asexual with sexual generation, in which the products of the one process differ from those of the other.

The *Hydrozoa* offer a complete series of gradations between those cases in which the term B is represented by a free, self-nourishing organism (*e.g.*, *Cyanæa*), through those in which it is free but unable to feed itself (*Calycophoridæ*), to those in which the sexual elements are developed in bodies which resemble free zooids, but are never detached, and are mere generative organs of the body on which they are developed (*Cordylophora*).

In the last case, the "individual" is the total product of

the development of the impregnated embryo, all the parts of which remain in material continuity with one another. The multiplication of mouths and stomachs in a *Cordylophora* no more makes it an aggregation of different individuals than the multiplication of segments and legs in a centipede converts that Arthropod into a compound animal. The *Cordylophora* is a differentiation of a whole into many parts, and the use of any terminology which implies that it results from the coalescence of many parts into a whole is to be deprecated.

In *Cordylophora* the generative organs are incapable of maintaining a separate existence; but in nearly allied *Hydrozoa* the unquestionable homologues of these organs become free zooids, in many cases capable of feeding and growing, and developing the sexual elements only after they have undergone considerable changes of form. Morphologically, the swarm of *Medusæ* thus set free from a Hydrozoon are as much organs of the latter, as the multitudinous pinnules of a *Comatula*, with their genital glands, are organs of the Echinoderm. Morphologically, therefore, the equivalent of the individual *Comatula* is the Hydrozoic stock plus all the *Medusæ* which proceed from it.

No doubt it sounds paradoxical to speak of a million of *Aphides*, for example, as parts of one morphological individual; but beyond the momentary shock of the paradox no harm is done. On the other hand, if the asexual *Aphides* are held to be individuals, it follows, as a logical consequence, not only that all the polypes on a *Cordylophora* tree are "feeding individuals," and all the genital sacs "generative individuals," while the stem must be a "stump individual," but that the eyes and legs of a lobster are "ocular" and "locomotive individuals." And this conception is not only somewhat more paradoxical than the other, but suggests a conception of the origin of the complexity of animal structure which is wholly inconsistent with fact.

IV. Ætiology.

Morphology, Distribution, and Physiology investigate and determine the facts of Biology. Ætiology has for its object the ascertainment of the causes of these facts, and the explanation of biological phenomena, by showing that they constitute particular cases of general physical laws. It is hardly needful to say that ætiology, as thus conceived, is in its infancy, and that the seething controversies, to which the attempt to found this branch of science made in the *Origin of Species* has given rise, cannot be dealt with in this place. At most, the general nature of the problems to be solved, and the course of inquiry needful for their solution, may be indicated.

In any investigation into the causes of the phenomena of life, the first question which arises is, whether we have any knowledge, and if so, what knowledge, of the origin of living matter?

In the case of all conspicuous and easily-studied organisms, it has been obvious, since the study of nature began, that living beings arise by generation from living beings of a like kind; but before the latter part of the 17th century, learned and unlearned alike shared the conviction that this rule was not of universal application, and that multitudes of the smaller and more obscure organisms were produced by the fermentation of not-living, and especially of putrefying dead matter, by what was then termed *generatio æquivoca* or *spontanea*, and is now called *abiogenesis*. Redi showed that the general belief was erroneous in a multitude of instances; Spallanzani added largely to the list; while the investigations of the scientific helminthologists of the present century have eliminated a further category of cases in which it was possible to doubt the applicability of the rule "*omne vivum e vivo*" to the more complex organisms which constitute the present fauna and flora of the earth. Even the most extravagant supporters of abiogenesis at the present day do not pretend that

organisms of higher rank than the lowest *Fungi*, and *Protozoa* are produced otherwise than by generation from pre-existing organisms. But it is pretended that *Bacteria*, *Torulæ*, certain *Fungi*, and "Monads" are developed under conditions which render it impossible that these organisms should have proceeded directly from living matter.

The experimental evidence adduced in favour of this proposition is always of one kind, and the reasoning on which the conclusion that abiogenesis occurs is based may be stated in the following form :—

All living matter is killed by being heated to *n* degrees.

The contents of a vessel, the entry of germs from without into which is prevented, have been heated to *n* degrees.

Therefore, all living matter which may have existed therein has been killed.

But living *Bacteria*, &c., have appeared in these contents subsequently to their being heated.

Therefore, they have been formed abiogenetically.

No objection can be taken to the logical form of this reasoning, but it is obvious that its applicability to any particular case depends entirely upon the validity, in that case, of the first and second propositions.

Suppose a fluid to be full of *Bacteria* in active motion, what evidence have we that they are killed when that fluid is heated to *n* degrees? There is but one kind of conclusive evidence, namely, that from that time forth no living *Bacteria* make their appearance in the liquid, supposing it to be properly protected from the intrusion of fresh *Bacteria*. The only other evidence, that, for example, which may be furnished by the cessation of the motion of the *Bacteria*, and such slight changes as our microscopes permit us to observe in their optical characters, is simply presumptive evidence of death, and no more conclusive than the stillness and paleness of a man in a swoon are proof that he is dead. And the caution is the more necessary in the case of *Bacteria*, since many of them naturally pass a considerable part of their existence in a condition

in which they show no marks of life whatever save growth and multiplication.

If indeed it could be proved that, in cases which are not open to doubt, living matter is always and invariably killed at precisely the same temperature, there might be some ground for the assumption, that, in those which are obscure, death must take place under the same circumstances. But what are the facts? It has already been pointed out, that leaving *Bacteria* aside, the range of high temperatures between the lowest, at which some living things are certainly killed, and the highest, at which others certainly live, is rather more than 100° Fahr., that is to say, between 104° Fahr. and 208° Fahr. It makes no sort of difference to the argument how living beings have come to be able to bear such a temperature as the last mentioned; the fact that they do so is sufficient to prove that, under certain conditions, such a temperature is not sufficient to destroy life.*

Thus it appears that there is no ground for the assumption that all living matter is killed at some given temperature between 104° and 208° Fahr.

No experimental evidence that a liquid may be heated to *n* degrees, and yet subsequently give rise to living organisms, is of the smallest value as proof that abiogenesis has taken place, and for two reasons:—Firstly, there is no proof that organisms of the kind in question are dead, except their permanent incapacity to grow and reproduce their kind; and secondly, since we know that conditions may largely modify the power of resistance of such organisms to heat, it is far more probable that such conditions existed in the experiment in question, than that the organisms were generated afresh out of dead matter.

Not only is the kind of evidence adduced in favour of abiogenesis logically insufficient to furnish proof of its occurrence, but it may be stated as a well-based induction,

* Messrs. Dallinger and Drysdale have recently shown good grounds for believing that the germs of some Monads are not destroyed by exposure to a temperature of 260° Fahr. or even 300° Fahr.

that the more careful the investigator, and the more complete his mastery over the endless practical difficulties which surround experimentation on this subject, the more certain are his experiments to give a negative result; while positive results are no less sure to crown the efforts of the clumsy and the careless.

It is argued that a belief in abiogenesis is a necessary corollary from the doctrine of Evolution. This may be true of the occurrence of abiogenesis at some time; but if the present day, or any recorded epoch of geological time, be in question, the exact contrary holds good. If all living beings have been evolved from pre-existing forms of life, it is enough that a single particle of living protoplasm should once have appeared on the globe, as the result of no matter what agency. In the eyes of a consistent evolutionist, any further independent formation of protoplasm would be sheer waste.

The production of living matter since the time of its first appearance, only by way of biogenesis, implies that the specific forms of the lower kinds of life have undergone but little change in the course of geological time, and this is said to be inconsistent with the doctrine of evolution. But, in the first place, the fact is not inconsistent with the doctrine of evolution properly understood, that doctrine being perfectly consistent with either the progression, the retrogression, or the stationary condition of any particular species for indefinite periods of time; and secondly, if it were, it would be so much the worse for the doctrine of evolution, inasmuch as it is unquestionably true, that certain, even highly organised, forms of life have persisted without any sensible change for very long periods. The *Terebratula psittacea* of the present day, for example, is not distinguishable from that of the Cretaceous epoch, while the highly organised Teleostean fish, *Beryx*, of the Chalk differed only in minute specific characters from that which now lives. Is it seriously suggested that the existing *Terebratulæ* and *Beryces* are not the lineal descendants of their Cretaceous ancestors, but that their modern represen-

tatives have been independently developed from primordial germs in the interval? But if this is too fantastic a suggestion for grave consideration, why are we to believe that the *Globigerinæ* of the present day are not lineally descended from the Cretaceous forms? And if their unchanged generations have succeeded one another for all the enormous time represented by the deposition of the Chalk and that of the Tertiary and Quaternary deposits, what difficulty is there in supposing that they may not have persisted unchanged for a greatly longer period?

The fact is, that at the present moment there is not a shadow of trustworthy direct evidence that abiogenesis does take place, or has taken place, within the period during which the existence of life on the globe is recorded. But it need hardly be pointed out, that the fact does not in the slightest degree interfere with any conclusion that may be arrived at, deductively, from other considerations that, at some time or other, abiogenesis must have taken place.

If the hypothesis of evolution is true, living matter must have arisen from not-living matter, for by the hypothesis, the condition of the globe was at one time such that living matter could not have existed in it,* life being entirely incompatible with the gaseous state. But living matter once originated, there is no necessity for another origination, since the hypothesis postulates the unlimited, though perhaps not indefinite, modifiability of such matter.

Of the causes which have led to the origination of living matter, then, it may be said that we know absolutely nothing. But postulating the existence of living matter endowed with that power of hereditary transmission, and with that tendency to vary which is found in all such matter, Mr. Darwin has shown good reasons for believing that the interaction between living matter and surround-

* It makes no difference if we adopt Sir W. Thomson's hypothesis, and suppose that the germs of living things have been transported to our globe from some other, seeing that there is as much reason for supposing that all stellar and planetary components of the universe are or have been gaseous, as that the earth has passed through this stage

ing conditions, which results in the survival of the fittest, is sufficient to account for the gradual evolution of plants and animals from their simplest to their most complicated forms, and for the known phenomena of Morphology, Physiology, and Distribution.

Mr. Darwin has further endeavoured to give a physical explanation of hereditary transmission by his hypothesis of Pangenesis; while he seeks for the principal, if not the only cause of variation in the influence of changing conditions.

It is on this point that the chief divergence exists among those who accept the doctrine of Evolution in its general outlines. Three views may be taken of the causes of variation:—

a. In virtue of its molecular structure, the organism may tend to vary. This variability may either be indefinite, or may be limited to certain directions by intrinsic conditions. In the former case, the result of the struggle for existence would be the survival of the fittest among an indefinite number of varieties; in the latter case, it would be the survival of the fittest among a certain set of varieties, the nature and number of which would be predetermined by the molecular structure of the organism.

b. The organism may have no intrinsic tendency to vary, but variation may be brought about by the influence of conditions external to it. And in this case also, the variability induced may be either indefinite or defined by intrinsic limitation.

c. The two former cases may be combined, and variation may to some extent depend upon intrinsic, and to some extent upon extrinsic, conditions.

At present it can hardly be said that such evidence as would justify the positive adoption of any one of these views exists.

If all living beings have come into existence by the gradual modification, through a long series of generations, of a primordial living matter, the phenomena of embryonic development ought to be explicable as particular cases of

the general law of hereditary transmission. On this view, a tadpole is first a fish, and then a tailed amphibian, provided with both gills and lungs, before it becomes a frog, because the frog was the last term in a series of modifications whereby some ancient fish became an urodele amphibian; and the urodele amphibian became an anurous amphibian. In fact, the development of the embryo is a recapitulation of the ancestral history of the species.

If this be so, it follows that the development of any organism should furnish the key to its ancestral history; and the attempt to decipher the full pedigree of organisms from so much of the family history as is recorded in their development has given rise to a special branch of biological speculation, termed *phylogeny*.

In practice, however, the reconstruction of the pedigree of a group from the developmental history of its existing members is fraught with difficulties. It is highly probable that the series of developmental stages of the individual organism never presents more than an abbreviated and condensed summary of ancestral conditions; while this summary is often strangely modified by variation and adaptation to conditions; and it must be confessed that, in most cases, we can do little better than guess what is genuine recapitulation of ancestral forms, and what is the effect of comparatively late adaptation.

The only perfectly safe foundation for the doctrine of Evolution lies in the historical, or rather archæological, evidence that particular organisms have arisen by the gradual modification of their predecessors, which is furnished by fossil remains. That evidence is daily increasing in amount and in weight; and it is to be hoped that the comparison of the actual pedigree of these organisms with the phenomena of their development may furnish some criterion by which the validity of phylogenetic conclusions, deduced from the facts of embryology alone, may be satisfactorily tested.

CHAPTER I.

I.—THE DISTINCTIVE CHARACTERS OF ANIMALS.

The more complicated forms of the living things, the general characters of which have now been discussed, appear to be readily distinguishable into widely separated groups, Animals and Plants. The latter have no power of locomotion and only rarely exhibit any distinct movement of their parts when these are irritated, mechanically or otherwise. They are devoid of any digestive cavity; and the matters which serve as their nutriment are absorbed in the gaseous and fluid state. Ordinary animals, on the contrary, not only possess conspicuous locomotive activity, but their parts readily alter their form or position when irritated. Their nutriment, consisting of other animals or of plants, is taken in the solid form into a digestive cavity.

But even without descending to the very lowest forms of animals and plants, we meet with facts which weaken the force of these apparently broad distinctions. Among animals, a coral or an oyster is as incapable of locomotion as an oak; and a tape-worm feeds by imbibition and not by the ingestion of solid matter. On the other hand, the Sensitive Plant and the Sundew exhibit movements on irritation, and the recent observations of Mr. Darwin and others leave little doubt that the so-called "insectivorous plants" really digest and assimilate the nutritive matters contained in the living animals which they catch and destroy. All the higher animals are dependent for the protein compounds which they contain upon other animals or upon plants. They are unable to manufacture protein out of simpler substances; and although positive proof is wanting that this incapacity extends to all animals, it may safely be

assumed to exist in all those forms of animal life which take in solid nutriment, or which live parasitically on other animals or plants, in situations in which they are provided with abundant supplies of protein in a dissolved state.

The great majority of the higher plants, on the contrary, are able to manufacture protein when supplied with carbonic acid, ammoniacal salts, water, and sundry mineral phosphates and sulphates: obtaining the carbon which they require by the decomposition of the carbonic acid, the oxygen of which is disengaged. One essential factor in the performance of this remarkable chemical process is the chlorophyll which these plants contain, and another is the sun's light.

Certain animals (*Infusoria, Cœlenterata, Turbellaria*) possess chlorophyll, but there is no evidence to show what part it plays in their economy. Some of the higher plants when parasitic, and a great group of the lower plants, the Fungi (which may be parasitic or not), are, however, devoid of chlorophyll, and are consequently totally unable to derive the carbon which they need from carbonic acid. Nevertheless they are sharply distinguished from animals, inasmuch as they are still, for the most part, manufacturers of protein. Thus such a Fungus as *Penicillium* is able to fabricate all the constituents of its body out of ammonium tartrate, sulphate and phosphate, dissolved in water (see *suprà*, p. 6, *note*); and the yeast-plant flourishes and multiplies with exceeding rapidity in water containing sugar, ammonium tartrate, potassium phosphate, calcium phosphate, and magnesium sulphate.

Nevertheless, the experiments of Mayer have shown that when peptones are substituted for the ammonium tartrate, the nutrition of the yeast-plant is favoured instead of being impeded. So that it would seem that the yeast-plant is able to take in protein compounds and assimilate them, as if it were an animal; and there can be no reasonable doubt that many parasitic Fungi, such as the *Botrytis Bassiana* of the silk-worm caterpillar, the *Empusa* of the house-fly, and, very probably, the *Peronospora*

of the potato-plant, directly assimilate the protein substances contained in the bodies of the plants and animals which they infest; nor is it clear that these Fungi are able to maintain themselves upon less fully elaborated nutriment.

Cellulose, amyloid and saccharine compounds were formerly supposed to be characteristically vegetable products; but cellulose is found in the tests of Ascidians; and amyloid and saccharine matters are of very wide, if not universal, occurrence in animals.

And on taking a comprehensive survey of the whole animal and vegetable worlds, the test of locomotion breaks down as completely as does that of nutrition. For it is the rule rather than the exception among the lowest plants, that at one stage or other of their existence they should be actively locomotive, their motor organs being usually *cilia*, altogether similar in character and function to the motor organs of the lowest animals. Moreover, the protoplasmic substance of the body in many of these plants exhibits rhythmically pulsating spaces or *contractile vacuoles* of the same nature as those characteristic of so many animals.

No better illustration of the impossibility of drawing any sharply defined distinction between animals and plants can be found, than that which is supplied by the history of what are commonly termed 'Monads.'

The name of 'Monad'* has been commonly applied to minute free or fixed, rounded or oval bodies, provided with one or more long cilia (*flagella*), and usually provided with a nucleus and a contractile vacuole. Of such bodies, all of which would properly come under the old group of *Monadidæ*, the history of a few has been completely worked out; and the result is that, while some (*e.g. Chlamydomonas*, zoospores of *Peronospora* and *Coleochæte*) are locomotive conditions of indubitable plants; others (*Radiolaria*, *Noctiluca*) are embryonic conditions of as indubitable animals. Yet others (zoospores of *Myxomycetes*) are embryonic forms of organisms which appear to be as much animals as plants;

* O. F. Müller, 'Historia Vermium,' 1773. "Vermis inconspicuus, simplicissimus, pellucidus, punctiformis."

inasmuch as in one condition they take in solid nutriment, and in another have the special morphological, if not physiological peculiarities of plants; while, lastly, in the case of such monads as those recently so carefully studied by Messrs. Dallinger and Drysdale, the morphological characters of which are on the whole animal, while their mode of nutrition is unknown, it is impossible to say whether they should be regarded as animals or as plants.

Thus, traced down to their lowest terms, the series of plant forms gradually lose more and more of their distinctive vegetable features, while the series of animal forms part with more and more of their distinctive animal characters, and the two series converge to a common term. The most characteristic morphological peculiarity of the plant is the investment of each of its component cells by a sac, the walls of which contain cellulose, or some closely analogous compound; and the most characteristic physiological peculiarity of the plant is its power of manufacturing protein from chemical compounds of a less complex nature. The most characteristic morphological peculiarity of the animal is the absence of any such cellulose investment.* The most characteristic physiological peculiarity of the animal is its want of power to manufacture protein out of simpler compounds.

The great majority of living things are at once referable to one of the two categories thus defined; but there are some in which the presence of one or other characteristic mark cannot be ascertained, and others which appear at different periods of their existence to belong to different categories.

* No analysis of the substance composing the cysts in which so many of the *Protozoa* inclose themselves temporarily, has yet been made. But it is not improbable that it may be analogous to *chitin*; and if so, it is worthy of remark that though chitin is a nitrogenous body, it readily yields a substance apparently identical with cellulose when heated with the double hyposulphite of copper and ammonia. It is possible, therefore, that the difference between the chitinous investment of an animal and the cellulose investment of a plant may depend upon the proportion of nitrogenous matter which is present in each case in addition to the chitin.

II.—THE MORPHOLOGICAL DIFFERENTIATION OF ANIMALS.

The simplest form of animal life imaginable would be a protoplasmic body, devoid of motility, maintaining itself by the ingestion of such proteinaceous, fatty, amyloid and mineral matters as might be brought into contact with it by external agencies; and increasing by simple extension of its mass. But no animal of this degree of simplicity is known to exist. The very humblest animals with which we are acquainted exhibit contractility, and not only increase in size, but, as they grow, divide, and thus undergo multiplication. In the simplest known animals—the *Protozoa* —the protoplasmic substance of the body does not become differentiated into discrete nucleated masses or cells, which by their metamorphosis give rise to the different tissues of which the adult body is composed. And, in the lowest of the *Protozoa*, the body has neither a constant form nor any further distinction of parts than a greater density of the peripheral, as compared with the central, part of the protoplasm. The first steps in complication are the appearance of one or more rhythmically contractile vacuoles, such as are found in some of the lower plants; and the segregation of part of the interior protoplasm as a rounded mass, the "endoplast" or "nucleus." Other *Protozoa* advance further and acquire permanent locomotive organs. These may be developed only on one part of the surface of the body, which may be modified into a special organ for their support. In some, a pedicle of attachment is formed, and the body may acquire a dense envelope (*Infusoria*), or secrete an internal skeleton of calcareous or silicious matter (*Foraminifera, Radiolaria*), or fabricate such a skeleton by gluing together extraneous particles (*Foraminifera*).

A mouth and gullet, with an anal aperture, may be formed, and the permeable soft central portion of the protoplasm may be so limited as to give rise to a virtual alimentary tract between these two apertures. The contractile vacuole

may be developed into a complicated system of canals (*Paramœcium*), and the endoplast may take on more and more definitely the characters of a reproductive organ, that is, may be the focus of origin of germs capable of reproducing the individual (*Vorticella*). In fact, rudiments of all the chief system of organs of the higher animals, with the exception, more or less doubtful, of the nervous, are thus sketched out in the *Protozoa*, just as the organs of the higher plants are sketched out in *Caulerpa*.

In the *Metazoa*, which constitute the rest of the animal kingdom, the animal, in its earliest condition, is a protoplasmic mass with a nucleus—is, in short, a Protozoon. But it never acquires the morphological complexity of its adult state by the direct metamorphosis of the protoplasmic matter of this nucleated body—the *ovum*—into the different tissues. On the contrary, the first step in the development of all the *Metazoa* is the conversion of the single nucleated body into an aggregation of such bodies of smaller size —the *Morula*—by a process of division, which usually takes place with great regularity, the ovum dividing first into two segments, which then subdivide, giving rise to four, eight, sixteen, &c., portions, which are the so-called *division masses* or *blastomeres*.

A similar process takes place in sundry *Protozoa* and gives rise to a protozoic aggregate, which is strictly comparable to the *Morula*. But the members of the protozoic aggregate become separate, or at any rate independent existences. What distinguishes the metazoic aggregate is that, though its component blastomeres also retain a certain degree of physiological independence, they remain united into one morphological whole, and their several metamorphoses are so ordered and related to one another, that they constitute members of a mutually dependent commonalty.

The *Metazoa* are the only animals which fall under common observation, and have therefore been known from the earliest times. All the higher languages possess general names equivalent to our beast, bird, reptile, fish,

insect and worm; and this shows the very early perception of the fact, that notwithstanding the wonderful diversity of animal forms, they are modelled upon comparatively few great types.

In the middle of the last century the founder of modern Taxonomy, Linnæus, distinguished animals into *Mammalia, Aves, Amphibia, Pisces, Insecta* and *Vermes*, that is to say, he converted common sense into science by defining and giving precision to the rough distinctions arrived at by ordinary observation.

At the end of the century, Lamarck made a most important advance in general morphology, by pointing out that mammals, birds, reptiles, and fishes, are formed upon one *type* or *common plan*, the essential character of which is the possession of a spinal column, interposed between a cerebro-spinal and a visceral cavity; and that in no other animals is the same plan of construction to be discerned. Hence he drew a broad distinction between the former and the latter, as the VERTEBRATA and the INVERTEBRATA. But the advance of knowledge respecting the structure of invertebrated animals, due chiefly to Swammerdam, Trembley, Réaumur, Peyssonel, Goeze, Roesel, Ellis, Fabricius, O. F. Müller, Lyonet, Pallas, and Cuvier, speedily proved that the *Invertebrata* are not framed upon one fundamental plan, but upon several; and, in 1795, Cuvier * showed that, at fewest, three morphological types, as distinct from one another as they are from that of the vertebrated animals, are distinguishable among the *Invertebrata*. These he named —I. Mollusques; II. Insectes et Vers; III. Zoophytes. In the 'Règne animal' (1816), these terms are Latinised, *Animalia Mollusca, Articulata,* and *Radiata*. Thus, says Cuvier: "It will be found that there exist four principal forms, four general plans, if it may thus be expressed, on which all animals appear to have been modelled; and the ulterior divisions of which, under whatever title naturalists may have designated them, are merely slight modifications, founded on the development or addition of certain parts.

* Tableau élémentaire de l'histoire des animaux. An vi.

These four common plans are those of the *Vertebrata*, the *Mollusca*, the *Articulata*, and the *Radiata*."

For extent, variety, and exactness of knowledge, Cuvier was, beyond all comparison, the greatest anatomist who has ever lived; but the absence of two conditions rendered it impossible that his survey of the animal kingdom should be exhaustive, grand and comprehensive as it was.

Up to the time of Cuvier's death in 1832, microscopic investigation was in its infancy, and hence the great majority of the lowest forms were either unknown or little understood; and it was only in the third decade of the present century that Rathke, Dollinger and Von Baer commenced that wonderful series of exact researches into embryology, which Von Baer organised into a special branch of morphology, developing all its most important consequences and raising it to its proper position, as the criterion of morphological theories.

Upon embryological grounds Von Baer arrived at the same conclusion as Cuvier, that there are four common plans of animal structure.

In the course of the last half-century the activity of anatomists and embryologists has been prodigious, and it may be reasonably doubted whether any form of animal life remains to be discovered which will not be found to accord with one or other of the common plans now known. But at the same time this increase of knowledge has abolished the broad lines of demarcation which formerly appeared to separate one common plan from another.

Even the hiatus between the *Vertebrata* and the *Invertebrata*, is partly, if not wholly, bridged over; and though among the *Invertebrata*, there is no difficulty in distinguishing the more completely differentiated representatives of such types or common plans as those of the *Arthropoda*, the *Annelida*, the *Mollusca*, the *Tunicata*, the *Echinodermata*, the *Cœlenterata*, and the *Porifera*, yet every year brings forth fresh evidence to the effect, that just as the plan of the plant is not absolutely distinct from that of the animal, so that of the Vertebrate has its points of community with

that of certain of the Invertebrates; that the Arthropod, the Mollusk, and the Echinoderm plans are united by that of the lower worms, and that the plan of the latter is separated by no very great differences, from that of the Cœlenterate and that of the Sponge.

Whatever speculative views may be held or rejected as to the origin of the diversities of animal form, the facts of anatomy and development compel the morphologist to regard the whole of the *Metazoa* as modifications of one actual or ideal primitive type, which is a sac with a double cellular wall, enclosing a central cavity and open at one end. This is what Haeckel terms a *Gastræa*. The inner wall of the sac is the hypoblast (*endoderm* of the adult), the outer the epiblast (*ectoderm*). Between the two, in all but the very lowest Metazoa, a third layer, the mesoblast (*mesoderm* of the adult), makes its appearance.

In the *Porifera*, the terminal aperture of the gastræa becomes the egestive opening of the adult animal, and the ingestive apertures are numerous secondary pore-like apertures formed by the separation of adjacent cells of the ectoderm and endoderm. The body may become variously branched, a fibrous or spicular endoskeleton is usually developed in the ectoderm, and no perivisceral cavity is developed. There are no appendages for locomotion or prehension; no nervous system nor sensory organs are known to exist; nor are there any circulatory, respiratory, renal, or generative organs.

In the *Cœlenterata*, the terminal aperture of the gastræa becomes the mouth, and if pores perforate the body walls, they do not subserve the ingestion of food. There is no separate perivisceral cavity, but, in many, an *enterocœle* or system of cavities, continuous with, but more or less separate from the digestive cavity, extends through the body. Prehensile appendages, *tentacula*, are developed in great variety. A chitinous exoskeleton appears in some, a calcareous or chitinous endoskeleton in others. There are no circulatory, respiratory, or renal organs (though it is possible that certain cells in the *Porpitæ, e.g.* may have an

uropoietic function); but special genital organs make their appearance, as do a definitely-arranged nervous system and organs of sense.

The lowest *Turbellaria* are on nearly the same grade of organisation as the lower *Cœlenterata*, but the thick mesoderm is traversed by canals which constitute a *water-vascular system*. In the adult state these canals open, on the one side, into the interstices of the mesodermal tissues, and, on the other, communicate with the exterior. Their analogy to the contractile vacuoles of the Infusoria on the one hand, and to the segmental organs of the Annelids on the other, lead me to think that they are formed by a splitting of the mesoblast, and that they thus represent that form of perivisceral cavity which I have termed a *schizocœle*. A nervous system consisting of a single or double ganglion with two principal longitudinal nerve cords, is found in many; and there may be eyes and auditory sacs.

Upon this foundation a gradual complication of form is based, brought about by—

1. The elongation of the bilaterally symmetrical body and the formation of a chitinous exoskeleton.

2. The development of a secondary aperture near the anterior end of the body, which becomes the permanent mouth.

3. The division of the mesoblast into successive segments (*somites*).

4. The development of two nervous ganglia in each somite.

5. The outgrowth of a pair of appendages from each somite, and their segmentation.

6. The gradual specialisation of the somites into cephalic, thoracic and abdominal groups; and that of their appendages into sense organs, jaws, locomotive limbs, and respiratory organs.

7. The conversion of the schizocœle into a spacious perivisceral cavity containing blood; the reduction of the water-vascular system and the appearance of pseudo-hæmal vessels; and the replacement of these, in the higher forms, by a heart, arteries, and veins, which contain blood.

8. The conversion of the simple inner sac of the gastræa into a highly complex alimentary canal, with special glandular appendages, representing the liver and the kidneys.

9. A similar differentiation of the genital apparatus.

10. A gradual complication of the eye, which, in its most perfect form, presents a series of crystal-clear conical rods, disposed perpendicularly to the transparent corneal region of the chitinous exoskeleton, and connected by their inner ends with the optic nerves of the præ-œsophageal ganglia.

By such modifications as these the plan of the simple Turbellarian gradually passes into that of the highest Arthropod.

Starting from the same point, if the mesoblast does not become distinctly segmented; if few, probably not more than three, pairs of ganglia are formed; if there are no segmented appendages, but the chief locomotive organ is a muscular foot developed in the neural aspect of the body; if, in the place of the chitinous exoskeleton, a shell is secreted by a specially modified part of the hæmal wall termed the mantle; if the schizocœle is converted into a blood cavity, which communicates with the exterior by an organ of Bojanus, which appears to represent the water-vascular system and the segmental organs; and if, along with these changes, the alimentary, circulatory, respiratory, genital, and sensory organs take on special characters, we arrive at the complete Molluscan plan.

From the Turbellarian to the Tunicate, or Ascidian, the passage is indicated, if not effected, by *Balanoglossus*, which, in its larval state, is comparable to an *Appendicularia* without its caudal appendage. On the other hand, the large pharynx of the *Tunicata* and the circle of tentacula around the oral aperture, with the single ganglion, approximate them to the *Polyzoa*. In the perforation of the pharynx by lateral apertures, which communicate with the exterior, either directly or by the intermediation of an atrial cavity, the *Tunicata* resemble only *Balanoglossus* and the *Vertebrata*. The axial skeleton of the caudal appendage has no parallel except in the vertebrate notochord. In the structure of

the heart and the regular reversal of the direction of its contractions, the *Tunicata* stand alone. The general presence of a test solidified by cellulose is a marked peculiarity, but in estimating its apparent singularity the existence of cellulose as a constituent of chitin must be remembered. Finally, the tadpole-like larvæ of many Ascidians are comparable only to the *Cercariæ* of Trematodes, on the one hand, and to vertebrate larval forms on the other.

Yet another apparently very distinct type is met with in the extensive group of the *Echinodermata*.

In all the other Metazoa, except the *Porifera* and *Cœlenterata*, the plan of the body is, obviously, bilaterally symmetrical, the halves of the body on each side of a median vertical plane being similar. Any disturbance of this symmetry, such as is found in some *Arthropoda* and in many *Mollusca*, arises from the predominant development of one half. But, in a Sea-urchin or Star-fish, five or more similar sets of parts are disposed around a longitudinal axis, which has the mouth at one end and the anus at the other; there is a radial symmetry, as in a sea anemone or a Ctenophoran. Nevertheless, close observation shows that, as is also the case in the Actinia or Ctenophoran, this radial symmetry is never perfect, and that the body is really bilaterally symmetrical in relation to a median plane which traverses the centre of length of one of the radiating metameres.

Another marked peculiarity of the Echinoderm type, is the general, if not universal, presence of a system of "ambulacral vessels" consisting of a circular canal around the mouth, whence canals usually arise and follow the middle line of each of the ambulacral metameres. And in the typical Echinoderm, these canals give off prolongations which enter certain diverticula of the body wall, the *pedicels* or suckers.

All Echinoderms have a calcareous endoskeleton.

In the chapter allotted to these animals, it will be shown

that they are modifications of the Turbellarian type, brought about by a singular series of changes undergone by the endoderm and mesoderm of the larva or Echinopædium

III.—THE PHYSIOLOGICAL DIFFERENTIATION OF ANIMALS, AND THE MORPHOLOGICAL DIFFERENTIATION OF THEIR ORGANS.

Regarded as machines for doing certain kinds of work, animals differ from one another in the extent to which this work is subdivided. Each subordinate group of actions or *functions* is allotted to a particular portion of the body, which thus becomes the organ of those functions, and the extent to which this division of physiological labour is carried differs in degree within the limits of each common plan, and is the chief cause of the diversity in the working out of the common plan of a group exhibited by its members. Moreover, there are certain types which never attain the same degree of physiological differentiation as others do.

Thus, some of the *Protozoa* attain a grade of physiological complexity as high as that which is reached by the lower *Metazoa*. And notwithstanding the multiplicity of its parts, no Echinoderm is so highly differentiated a physiological machine as is a snail.

A mill with ten pairs of millstones need not be a more complicated machine than a mill with one pair; but if a mill have two pairs of millstones, one for coarse and one for fine grinding, so arranged that the substance ground passes from one to the other, then it is a more complicated machine—a machine of higher order—than that with ten pairs of similar grindstones. In other words, it is not mere multiplication of organs which constitutes physiological differentiation; but the multiplication of organs for different functions in the first place, and the degree in which they are co-ordinated, so as to work to a common end, in the second place. Thus, a lobster is a higher animal, from a physiological point of view, than a *Cyclops*, not

because it has more distinguishable organs, but because these organs are so modified as to perform a much greater variety of functions, while they are all co-ordinated towards the maintenance of the animal, by its well-developed nervous system and sense organs. But it is impossible to say that *e.g.* the *Arthropoda*, as a whole, are physiologically higher than the *Mollusca*, inasmuch as the simplest embodiments of the common plan of the Arthropoda are less differentiated physiologically than the great majority of Mollusks.

I may now rapidly indicate the mode in which physiological differentiation is effected in the different groups of organs of the body among the Metazoa.

Integumentary Organs.—In the lowest *Metazoa*, the integument and the ectoderm are identical, but so soon as a mesoderm is developed, the layer of the mesoderm which is in contact with the ectoderm becomes virtually part of the integument, and in all the higher animals is distinguished as the *dermis* (*enderon*), while the ectodermal cells constitute the *epidermis* (*ecderon*). The connective tissue and muscles of the integument are exclusively developed in the enderon, while, from the epidermis, all cuticular and cellular exoskeletal parts, and all the integumentary glands are developed. The latter are always involutions of the epidermis. The hard protective skeletons in all invertebrate *Metazoa*, except the *Porifera*, the *Actinozoa*, the *Echinodermata*, and the *Tunicata*, are cuticular structures, which may be variously impregnated with calcareous salts formed on the outer surface of the epidermic cells.

In the *Porifera*, the calcareous or silicious deposit takes place within the ectoderm itself, and, probably, the same process occurs, to a greater or less extent, in the *Actinozoa*. In those *Tunicata* which possess a test, it appears to be a structure *sui generis*, consisting of a gelatinous basis excreted by the ectoderm, in which cells detached from the ectoderm divide, multiply, and give rise to a deposit of cellulose. The test may take on the structure of cartilage or even of

connective tissue. In the *Vertebrata* alone do we find hard exoskeletal parts formed by the cornification and cohesion of epidermic cells.

In the *Actinozoa* and the *Echinodermata*, the hard skeleton is, in the main, though perhaps not wholly, the result of calcification of elements of the mesoderm. In some Mollusks, portions of the mesoderm are converted into true cartilage, while the enderon of the integument often becomes the seat of calcareous deposit. The endoskeleton and the dermal exoskeleton of the *Vertebrata* are cellular (cartilage, notochord) or fibrous (connective tissue) modification of the mesoderm, which may become calcified (bone, dentine). Recent investigations tend to show that the enamel of the teeth is derived from the ectoderm.

The Alimentary Apparatus.—From the simple sac of the *Hydra* or aproctous *Turbellarian*, we pass to the tubular alimentary tract of the proctuchous *Turbellaria*. In the *Rotifera* and *Polyzoa*, there is a marked distinction into buccal cavity, pharynx, œsophagus, stomach and intestines; while distinct salivary, hepatic, and renal glands, are found in the majority of the higher invertebrates, and, not unfrequently, glands secreting an odorous, or coloured fluid, appear in the region of the termination of the alimentary canal.

The oral and gastric regions are armed with cuticular teeth in many *Invertebrata*; but teeth formed by the calcification of papillary elevations of the enderon of the lining of the mouth, are confined to the *Vertebrata*; unless, as seems probable, the teeth of the *Echinidea* have a similar origin.

The lining membrane of the oral cavity is capable of being everted, as a proboscis, in many *Invertebrata*. The margins of the mouth may be raised into folds, armed with cuticular plates. In the *Vertebrata*, the jaws are such folds, supported by endoskeletal cartilages, belonging to the system of the visceral arches, or by bones developed in and around them; but, in the *Arthropoda*, what are usually termed jaws are modified limbs.

The Blood and Circulatory Apparatus.—In the *Cœlenterata*, the somatic cavity, or enterocœle, is in free communication with the digestive cavity, and not unfrequently communicates with the exterior by other apertures. The fluid which it contains represents blood; it is moved by the contractions of the body, and, generally, by cilia developed on the endodermal lining of the enterocœle. In the *Turbellaria*, *Trematoda* and *Cestoidea*, the lacunæ of the mesoderm and the interstitial fluid of its tissues are the only representatives of a blood-vascular system. It is probable that these communicate directly with the terminal ramifications of the water-vascular system. In the *Rotifera*, a spacious perivisceral cavity separates the mesoderm into two layers, the *splanchnopleure*, which forms the enderon of the alimentary canal, and the *somatopleure*, which constitutes the enderon of the integument. The terminations of the water vessels open into this cavity. In Annelids, there is a similar perivisceral cavity communicating in the same way with the segmental organs; but, in most, there is, in addition, a system of canals with contractile walls, which, in some, communicate freely with the perivisceral cavity; but, in the majority, are shut off from it. These canals are filled by a clear, usually non-corpusculated fluid, which may be red or green, and constitute the *pseud-hæmal* system. The fluid which occupies the perivisceral cavity contains nucleated corpuscles, and has the characters of ordinary blood. It seems probable that the fluid of the pseud-hæmal vessels, as it contains a substance resembling hæmoglobin, represents a sort of respiratory blood.

In the *Arthropoda*, no segmental organs or pseud-hæmal vessels are known. In the lowest forms, the perivisceral cavity and the interstices of the tissues represent the whole blood system, and colourless blood cells float in their fluid contents. In the higher forms, a valvular heart, with arteries and capillaries, appears, but the venous system remains more or less lacunar. In the *Mollusca*, the same gradual differentiation of the blood-vascular system is observable. In very many, if not all, the blood cavities communicate directly with the exterior by the 'organs of

Bojanus'—which resemble very simple segmental organs, and appear to be always associated with the renal apparatus.

In the *Vertebrata*, *Amphioxus* has a system of blood vessels with contractile walls, and no distinct heart. In all the other Vertebrates there is a heart with at fewest three chambers (*sinus venosus, atrium, ventricle*), arteries, capillaries, and veins, and a system of lymphatic vessels connected with the veins. The lymphatic fluid consists of a colourless plasma, with equally colourless nucleated corpuscles, the blood plasma contains, in addition, red corpuscles, which are nucleated in *Ichthyopsida* and *Sauropsida*, but have no nucleus in the *Mammalia*. The lymphatic vessels always communicate with the interstitial lacunæ of the tissues, and, in the lower Vertebrates are themselves, to a great extent, irregular sinuses. The venous system presents many large sinuses in the lower vertebrates; while, in the higher forms, these sinuses are for the most part replaced by definite vessels with muscular walls. But the "serous cavities" remain as vast lymphatic lacunæ. Valves make their appearance in the lymphatics and in the veins, and the heart becomes subdivided in such a manner as to bring about a more and more complete separation of the systemic circulatory apparatus from that which supplies the respiratory organs.

The Respiratory System.—In the lower *Metazoa* respiration is effected by the general surface of the body In the Annelids, processes of the integument, which are sometimes branched and usually are abundantly ciliated and supplied with pseud-hæmal vessels, give rise to *branchiæ*. Branchiæ, abundantly supplied with blood-vessels, but never ciliated, attain a great development in the *Crustacea*. The access of fresh water to them is secured by their attachment to some of the limbs; and, in the higher Crustaceans, one of the appendages, the second maxilla, serves as an accessory organ of respiration. Although especially adapted for aquatic respiration, they are converted into air-breathing organs in the land crabs, being protected and kept moist in a large chamber formed by the carapace.

In some mollusks (*e.g. Pteropoda*), the delicate lining membrane of the pallial cavity serves as the respiratory organ, but, in most, branched or laminated processes of the body give rise to distinct branchiæ. The mantle becomes an accessory organ of respiration, being so modified as to direct, or to cause, the flow of currents of water over the branchiæ contained in its cavity. In many adult urodele *Amphibia* (*Perennibranchiata*), and in the embryonic condition of all *Amphibia* and of many fishes, branchiæ of a similar character, abundantly supplied with blood vessels, are attached to more or fewer of the visceral arches.

In all these cases the branchiæ are external, and are developed from the integument. In Crustaceans and Mollusks the blood with which they are supplied is returning to the heart; while, in the *Vertebrata* mentioned, it is flowing from the heart, and it will be observed that the gradual perfectioning of the respiratory machinery consists, first, in the outgrowth of parts of the integument specially adapted to subserve the interchange between the gases contained in the blood and those in the surrounding medium; secondly, in the increase of the surface of the branchiæ, so as to enable them to do their work more rapidly; thirdly, in the development of accessory organs, by which the flow of water over the branchiæ is rendered definite and constant, and may be increased or diminished in accordance with the needs of the œconomy.

It is probable that the water-vascular system and the segmental organs of Turbellarians and Annelids, the cloacal tubes of the *Gephyrea* and of some *Holothuridea*; the ambulacral vesicles of the Echinoderms, and the large pharyngeal cavity of the *Polyzoa*; to a greater or less extent, subserve respiration, and constitute internal respiratory organs.

In *Myriapoda* and *Insecta*, the *tracheæ*—tubes which open on the surface of the body and contain air, and are curiously similar in their distribution to the water vessels of the worms—constitute a very complete internal aerial respiratory apparatus.

In *Arachnida*, tracheæ may exist alone, or be accompanied

by folded *pulmonary sacs*, or the latter may exist alone, as in the Scorpion. In this case, these lungs are supplied by blood which is returning from the heart.

In these animals, the flow of air into and out of the air cavities is governed by the contractions of muscles of the body, disposed so as to alter its vertical and longitudinal dimensions. In the higher forms, the entrance and exit of air is regulated by valves, placed at the external openings (*stigmata*) of the tracheæ, and provided with muscles, by which they can be shut.

In the *Enteropneusta* and the *Tunicata* a new form of internal aquatic respiratory apparatus appears. The large pharynx is perforated by lateral apertures, which place its cavity in communication with the exterior; and water, taken in by the mouth, is driven through these branchial clefts and aerates the blood, which circulates in their interspaces.

The respiratory apparatus of *Amphioxus*, of all adult fishes, and of the tadpoles of the higher anurous *Amphibia*, in a certain stage of their existence, is of an essentially similar character. The accessory respiratory apparatus for the maintenance and the regulation of the currents of water over the gills is furnished by the visceral arches and their muscles; and the respiratory blood flows from the heart.

In Mollusks which live on land (*Pulmogasteropoda*), the lining wall of the mantle cavity becomes folded and highly vascular, and subserves the aeration of the venous blood, which flows through it on its way to the heart. The lung is here a modification of the integument, and might be termed an *external lung*. The lungs of the air-breathing *Vertebrata*, on the contrary, are diverticula of the alimentary canal, posterior to the hindermost of the visceral arches. They receive their blood from the hindermost aortic arch. It therefore flows from the heart. The gradual improvement of these lungs as respiratory machines is effected, first, by the increase of the surface over which the venous blood brought to the lungs is distributed; secondly, by changes in the walls of the cavity in which

the lungs are contained, by which that cavity gradually becomes shut off from the peritoneal chamber, and divided from it by a muscular partition. Concurrently with these modifications, a series of alterations takes place in the accessory apparatus of respiration, whereby the machinery of inspiration, which, in the lower *Vertebrata*, is a buccal force-pump, which drives air into the lungs, in the same way as water is driven through the branchiæ, is replaced by a thoracic suction-pump, which draws air into the lungs by dilatation of the walls of the closed cavity in which they are contained. Along with these changes, modifications of the heart take place, in virtue of which one half of its total mechanical power becomes more and more exclusively appropriated to the task of driving the blood through the lungs. The term 'double circulation' applied to the course of the blood in the highest *Vertebrata* is, however, a misnomer. In the highest, as in the lowest, of these animals, the blood completes but one circle, and the respiratory organ is in the course of the outward current.

Many animals are truly amphibious, combining aquatic and aerial respiratory organs.

Thus, among Mollusks, *Ampullaria* and *Onchidium* combine branchiæ with pulmonary organs; many Teleostean fishes have the lining membrane of the enlarged branchial chamber vascular and competent to subserve aerial respiration. And in the *Ganoids* and *Teleostei*, the presence of an air bladder, which is both functionally and morphologically of the same nature as a lung, is very common. But, in the majority of the *Teleostei*, the air bladder is turned aside from its pulmonary function to subserve mechanical purposes, in affecting the specific gravity of the body. On the other hand, in the *Ganoids* and *Dipnoi*, the whole series of modifications by which the air bladder passes into the lung are patent. In such lower *Amphibia* as *Proteus* and *Menobranchus*, branchial respiration is predominant, and the lungs are subsidiary; but in the higher, the lungs acquire greater importance, while the branchiæ diminish, and eventually disappear.

The *Uropoietic System.*—Uropoietic organs, distinct from the alimentary canal, are probably represented by the water-vascular system and segmental organs of the worms. The 'organs of Bojanus' of Mollusks are sacs or tubes opening, on the one side, on the exterior of the body, and, on the other, into some part of the blood-vascular system. So far, as Gegenbaur has shown, they resemble the segmental organs of Annelids. In the majority of the *Mollusca*, some part of the wall of the organ of Bojanus is in close relation with the venous system near the heart, and the nitrogenous waste of the body is here eliminated from the venous blood. In the *Vertebrata*, the renal apparatus is constructed on the same principle. If for simplicity's sake we reduce a mammalian kidney to an ureter with a single uriniferous tubule, it corresponds with an organ of Bojanus, so far as it contains a cavity communicating with the exterior at one end, and having a vascular plexus—the Malpighian body—in intimate contact with the opposite end In the adult mammal there is no direct communication between the urinary duct and the blood-vascular system. But, inasmuch as recent researches have proved that the ureter is formed by subdivision of the Wolffian duct, and that the Wolffian duct is primitively a diverticulum of the peritoneal cavity, and remains for a longer or shorter time (permanently, in some of the lower Vertebrata, as *Myxine*) in communication therewith; and since it has further been shown that the peritoneal cavity communicates directly with the lymphatics, and therefore indirectly with the veins; it follows that the vertebrate kidney is an extreme modification of an organ, the primitive type of which is to be found in the organ of Bojanus of the Mollusk, and in the segmental organ of the Annelid; and, to go still lower, in the water-vascular system of the Turbellarian. And this, in its lowest form, is so similar to the more complex conditions of the contractile vacuole of a Protozoon, that it is hardly straining analogy too far to regard the latter as the primary form of uropoietic as well as of internal respiratory apparatus.

The Nervous System.—In its essential nature, a nerve is a definite tract of living substance, through which the molecular changes which occur in any one part of the organism are conveyed to and affect some other part Thus, if, in the simple protoplasmic body of a Protozoon, a stimulus applied to one part of the body, were more readily transmitted to some other part, along a particular tract of the protoplasm, that tract would be a virtual nerve, although it might have no optical or chemical characters which should enable us to distinguish it from the rest of the protoplasm.

It is important to have this definition of nerve clearly before us in considering the question whether the lowest animals possess nerves or not. Assuredly nothing of the kind is discernible, by such means of investigation as we at present possess, in *Protozoa* or *Porifera*; but any one who has attentively watched the ways of a *Colpoda*, or still more of a *Vorticella*, will probably hesitate to deny that they possess some apparatus, by which external agencies give rise to localised and co-ordinated movements. And when we reflect that the essential elements of the highest nervous system—the fibrils into which the axis fibres break up—are filaments of the extremest tenuity, devoid of any definite structural or other characters, and that the nervous system of animals only becomes conspicuous by the gathering together of these filaments into nerve fibres and nerves, it will be obvious that there are as strong morphological, as there are physiological, grounds for suspecting that a nervous system may exist very low down in the animal scale, and possibly even in plants.

The researches of Kleinenberg, which may be readily verified, have shown that, in the common *Hydra*, the inner ends of the cells of the ectoderm are prolonged into delicate processes, which are eventually continued into very fine longitudinal filaments, forming a layer between the ectoderm and the endoderm.

Kleinenberg terms these neuro-muscular elements, and thinks that they represent both nerve and muscle in their

undifferentiated state. But it appears to me that while the assumed contractility of these fibres might account for the shortening of the body of the Polype, they can have nothing to do with its lengthening. As the latter movements are at least as vigorous as the former, we are therefore obliged to assume sufficient contractility in the general constituents of the body to account for them. And if so, what ground is there for supposing that this contractility can be exerted by only one tissue when the body shortens? To my mind, it is more probable that "Kleinenberg's fibres" are solely internuncial in function, and therefore the primary form of nerve. The prolongations of the ectodermal cells have indeed a strangely close resemblance to those of the cells of the olfactory and other sense organs in the *Vertebrata*; and it seems probable that they are the channels by which impulses affecting any of the cells of the ectoderm are conveyed to other cells and excite their contraction.

The researches of Eimer* upon the nervous system of the *Ctenophora* are in perfect accordance with this view. The mesoderm is traversed in all directions by very fine fibrils, varying in diameter from $\frac{1}{30000}$ to $\frac{1}{2500}$ of an inch. These fibrils present numerous minute varicosities, and, at intervals, larger swellings which contain nuclei, each with a large and strongly refracting nucleolus. These fibrils take a straight course, branch dichotomously, and end in still finer filaments, which also divide, but become no smaller. They terminate partly in ganglionic cells, partly in muscular fibres, partly in the cells of the ectoderm and endoderm. Many of the nerve fibrils take a longitudinal course beneath the centre of each series of paddles, and these are accompanied by ganglionic cells, which become particularly abundant towards the aboral end of each series. The eight bands meet in a central tract at the aboral pole of the body; but Eimer doubts the nervous nature of the cellular mass which lies beneath the lithocyst and supports the eye-spots.

* 'Zoologische Studien auf Capri.' Leipzig, 1873.

The nervous system of the Ctenophoran is, therefore, just such as would arise in *Hydra*, if the development of a thick mesoderm gave rise to the separation and elongation of Kleinenberg's fibres; and if special bands of such fibres, developed in relation with the chief organs of locomotion, united in a central tract directly connected with the higher sensory organs. We have here, in short, virtual, though incompletely differentiated, brain and nerves.

All recent investigation tends more and more completely to establish the following conclusions: firstly, that the central ganglia of the nervous system in all animals are derived from the ectoderm; secondly, that all the nerves of the sensory organs terminate in cells of the ectoderm; thirdly, that all motor nerves end in the substance of the muscular fibres to which they are distributed. So that, in the highest animals, the nervous system is essentially similar to that of the lowest; the difference consisting, in part, in the proportional size of the nerve centres, and, in part, in the gathering together of the internuncial filaments into bundles, having a definite arrangement, which are the *nerves*, in the ordinary anatomical sense of the term.

And as respects the ectodermal cells which constitute the fundamental part of the organs of the special senses, it is becoming clear that the more perfect the sensory apparatus, the more completely do these sensigenous cells take on the form of delicate rods or filaments. Whether we consider the organs of the lateral line in Fishes and Amphibia; the gustatory bulbs; the olfactory cells; the auditory cells; or the elements of the retina, this rule holds good.

Every one of the organs of the higher senses makes its appearance in the animal series as a part of the ectoderm, the cells of which have undergone a slight modification. In the case of the eye, accessory structures, consisting of variously-coloured masses of pigment, which surround the visual cells, and of a transparent refracting cuticular or cellular structure which lies superficially to them—a rudimentary choroid and cornea—are next added. The highest form of compound Arthropod eye differs from this only in

the differentiation of the layer of sensigenous cells into the crystalline cones and their appendages, and it has not been clearly made out that the simple eyes of most other *Invertebrata* have undergone any further change.

But in *Nautilus* the nerve cells and choroid line the walls of a deep cup open externally; which, though its development has not been traced, may be safely assumed to result from the involution of the retinal ectoderm. It may be compared to an arthropod compound eye become concave instead of convex.

In the higher *Cephalopoda*, the margins of the ocular pouch unite and give rise to a true cornea, which, however, frequently remains perforated; and a crystalline lens is developed. In the higher *Vertebrata* the retina is still a modified portion of the ectoderm For inasmuch as the anterior cerebral vesicle is formed by involution of the epiblast, and the optic vesicle is a diverticulum of the anterior cerebral vesicle—it necessarily follows that the outer wall of the optic vesicle is really part of the ectoderm, its inner face being, morphologically, a portion of the surface of the body. The rods and cones of the vertebrate eye, therefore, exactly correspond with the crystalline cones, &c., of the Arthropod eye; and the reversal of the ends which are turned towards the light in the *Vertebrata*, is a necessary result of the extraordinary change of position which the retinal surface undergoes in them.

In the part of the ectoderm which takes on the auditory function, two kinds of accessory organs, solid particles suspended in a fluid and fine hair-like filaments, are developed in close relation with the nerve endings. In the *Crustacea* both are combined, and an involution of the sensory region takes place, which usually remains open throughout life, and represents the most rudimentary form of auditory labyrinth. The Crustacean ear is the parallel of the *Nautilus* eye. In the *Vertebrata*, the membranous labyrinth is similarly an involution of the integument, which remains open throughout life in many Fishes, but becomes shut off and surrounded by thick mesoblastic structures in

all the higher *Vertebrata*. The *tympanum* and the *ossicula auditus* are additional accessory structures, formed at the expense of the hyomandibular cleft and its boundary walls

The Reproductive System.—The relation of the reproductive elements to the primitive layers of the germ, is as yet uncertain. E. van Beneden has brought forward very strong evidence to the effect that in *Hydractinia*, the spermatozoa are modified cells of the ectoderm, and the ova of those of the endoderm; but whether it can be safely concluded that this rule holds good for animals generally, is a question that can only be settled by much and difficult investigation. The fact that, in the *Vertebrata*, the ova and spermatozoa are products of the epithelial lining of the peritoneal cavity, and therefore proceed from the mesoblast, appears at first sight directly to negative any such generalisation. But it must be remembered that the origin of the mesoblast itself is yet uncertain, and that it is quite possible that one portion of that layer may originate in the ectoderm and another in the endoderm

There is some reason to suspect that hermaphrodism was the primitive condition of the sexual apparatus, and that unisexuality is the result of the abortion of the organs of the other sex, in males and females respectively.

Very low down in the animal series, among the *Turbellaria*, the accessory organs of generation acquire a great complexity. In the lower *Turbellaria* the excretory duct is a mere short wide passage. But, in the higher *Turbellaria* and *Trematoda*, the female apparatus presents a germarium, in which the ova are developed; vitellarian glands, which give rise to a supplemental or food yelk; an oviduct; a uterus and vagina; and a spermatheca, in which the semen is stored up. The male apparatus presents a testis, a vas deferens, and a penis. The function of the vitellarian gland may be taken on by cells of the ovary, or oviduct, or accessory yelk substance may be formed within the primitive ovum itself, in the *Arthropoda* and in most *Mollusca*, but the reproductive organs in all these animals are reducible to the Turbellarian type.

In the Annelids (*Oligochæta* and *Polychæta*), the ovaria and testes often have no special ducts, and their products make their way out of the body by canals which appear to be modified segmental organs.

In the *Cephalopoda*, again, the ovaria and testes part with their contents by dehiscence into chambers connected with the water cavities, which are prolongations of the organs of Bojanus. And they are conveyed away from these chambers by ducts, the oviducts or vasa deferentia, which commence by open mouths in them.

In the *Vertebrata*, the reproductive organs either dehisce and pour their contents into the peritoneal cavity, whence they are conveyed outwards by abdominal pores (*Marsipobranchii*, many *Teleostei*), or they are continued into ducts which open behind the anus separately from the renal opening in the females, but in common with it in the males (most Teleosteans); or their ducts are derived from portions of the primitive renal apparatus which, as we have seen, is a structure of the same order as the organs of Bojanus and the segmental organs. The testis is usually converted into a mass of tubuli, which eventually open directly into the ducts (*epididymis*, *vas deferens*) derived from the renal organs. The ovary, on the other hand, becomes an aggregation of sacs—the Graafian follicles—and the oviducts open into the peritoneal cavity.

Development.—The embryo either passes through all stages from the morula to a condition differing from the adult only in size, proportions, and sexual characters, or it leaves the egg in a condition more or less remote from the adult state, and sometimes exceedingly different from it. In the latter case, the animal is said to undergo a *metamorphosis*. Each of these modes of development occurs in members of the same group, and often in closely allied forms: as, for example, the former in the crayfish (*Astacus*), and the latter in the lobster (*Homarus*).

When metamorphosis occours, the larva may live under conditions totally different from those under which the adult passes its existence, and its structure may be variously

modified in relation to these conditions. Thus the larva of an animal which is fixed in the adult state may be provided with largely developed locomotive organs; while that of an adult which feeds by suction may be provided with powerful apparatus for the seizure and manducation of vegetable and animal prey.

The larva of a free adult may be parasitic, or that of a parasitic adult free and actively locomotive. Moreover, the whole course of development may take place outside the body of the parent, or more or less extensively within it, whence the distinction of *oviparous*, *ovoviviparous*, and *viviparous* * animals.

Finally, when development takes place within the body of the parent, the fœtus may receive nourishment from the latter by means of an apparatus termed a *placenta*, by which an exchange between the parental and fœtal blood is readily effected. Examples of placentæ are found not only in the higher mammals, but in some Plagiostome fishes and among the *Tunicata*.

In many Insects and in the higher Vertebrates, the embryo acquires a special protective envelope, the *amnion*, which is thrown off at birth; while, in many Vertebrates, another fœtal appendage, the *allantois*, subserves the respiration and nutrition of the fœtus.

The strange phenomena included under the head of the Alternation of Generations, and which result from the division, by budding or otherwise, of the embryo which leaves the egg, into a succession of independent zooids, only the last of which acquires sexual organs, have already been generally discussed.

* As eggs capable of development are alive, this terminology is etymologically bad; and *ovoviviparous* is particularly objectionable, as all animals bring forth live eggs or that which proceeds from them. But as understood to apply to animals which lay eggs; to those in which the eggs are hatched within the interior of the body, without any special fœtal nutritive apparatus; and to those in which the young are provided with such an apparatus, they have a certain convenience.

IV.—THE DISTRIBUTION OF ANIMALS.

The distribution of animals has to be considered under two points of view; first, in respect of the present condition of nature, and secondly, in respect of past conditions. The first is commonly termed *Geographical*, the second *Geological*, or *Palæontological, Distribution.* A little consideration, however, will show that this classification of the facts of distribution is essentially faulty, inasmuch as many of the phenomena included under the second head are of the same order as those comprehended under the first. Zoological Distribution comprehends all the facts which relate to the occurrence of animals upon the earth's surface, throughout the time during which animal life has existed on the globe. Therefore it embraces—

First, *Zoological Chronology*, or the duration and order of succession of living forms in time; and—

Secondly, *Zoological Geography*, or the distribution of life on the earth's surface at any given epoch.

What is commonly termed Geographical Distribution, is simply that distribution which obtains at the present epoch; but it is obvious, that at any given moment in their past history, animals must have had some sort of geographical distribution; and considerable acquaintance with the nature of that distribution has now been obtained for all the epochs, the nature of the living population of which has been revealed by fossil remains. I do not propose to deal at length with either branch of distribution in this place, but a few broad truths which have been established may be mentioned.

Geographical Distribution at the present epoch.—The Fauna of the deep sea (below 500 fathoms) has been shown by the investigations of Wyville Thomson and his associates of the 'Challenger,' to present a striking general uniformity in all parts of the world hitherto explored, in correspondence with the general uniformity of conditions at such depths.

With respect to the surface of the sea, the observations of the same naturalists tend to establish a like uniformity of the great types of Foraminiferal life throughout the tropical and temperate zones—with a diminution in the abundance of that life towards the arctic and antarctic regions, where it appears to be replaced by *Radiolaria* and Diatomaceous plants.

With regard to higher organisms, the oceanic *Hydrozoa* and the *Ctenophora* are undoubtedly very widely spread. It is probable that they attain their maximum development in warm seas, though the known facts are insufficient for the definite conclusion. *Sagitta* and *Appendicularia*, with many genera of *Copepoda*, *Crustacea*, and *Pteropoda*, are of world-wide distribution; and it is at present doubtful whether any well-marked provinces of the ocean can be defined by the occurrence of purely pelagic animals. On the other hand, shallow-water marine animals fall into assemblages characteristic of definite areas or *provinces of distribution*—that is to say, though many species have a world-wide distribution, others occur only in particular localities, and certain geographical areas are marked by the existence in them of a number of such peculiar species. The basins of the Pacific, the Indian Ocean, the Atlantic, the Mediterranean, and the Arctic seas, are thus especially characterised; and even limited areas of these great geographical divisions, such as the Celtic, the Lusitanian, and the Australian, have their peculiar features.

But though the shallow-water marine Faunæ thus follow the broad features of physical geography, and though, within each great province of distribution thus marked out, temperature and other physical conditions have an obvious influence in determining the range of species; yet, on comparing any two great areas together, differences in climatal conditions are at once seen to be inadequate to account for the differences between the Faunæ of the two areas. Climate in no way enables us to understand why the *Trigonia*, the pearly *Nautilus*, the *Cestracion*, the eared seals, and the penguins are found in the Pacific.

and not in the Atlantic area;* nor why the *Cetacea* of the arctic and antarctic regions should be as different as they are. When we turn to the distribution of land animals, the boundaries of the provinces of distribution correspond neither with physical features nor with climatic conditions. Mammals, birds, reptiles, and amphibians are so distributed at the present day as to mark out four great areas or provinces of distribution of very unequal extent, in each of which a number of characteristic types, not found elsewhere, occur. These are, 1. The *Arctogœal*, including North America, Europe, Africa, and Asia as far as Wallace's line, or the boundary between the Indian and the Papuan divisions of the Indian Archipelago. 2. The *Austrocolumbian*, comprising all the American continent south of Mexico. 3. The *Australian*, from Wallace's line to Tasmania. 4. The *Novozelanian*, including the islands of New Zealand.†

There is now no doubt that provinces of distribution, closely corresponding with these, existed at the time of the Quaternary and later Tertiary rocks. In Europe, North America, and Asia, the Arctogœal province was as distinctly characterised in the Miocene, and probably in the Eocene epoch, as it is at present. What may have been the case in Austrocolumbia, Australasia, and Novozelania we have no means of being certain, in the absence of sufficient knowledge of the Miocene and Eocene deposits of those regions.

Our present knowledge of the geographical distribution which obtained in the older periods, does not enable us to speak with any confidence as to the limits of the provinces of distribution in the past. But this much is certain, that as far back as the epoch of the Trias—at the dawn of the

* Penguins are found at the Cape of Good Hope and at the Falkland Islands, but not in the northern parts of the West Coast of Africa, nor of the East Coast of South America. In the Pacific they stretch north to the Papuan and Peruvian coasts.

† On the classification and distribution of the *Alectoromorphæ* and *Heteromorphæ*: Proceedings of the Zoological Society, 1868. Sclater on the 'Geographical Distribution of Birds.' Ibid vol. ii. Pucheran, 'Revue et Magasin de Zoologie,' 18-5 Murray, 'The Geographical Distribution of Mammals.'

Secondary period—the *Reptilia* and *Amphibia* of Europe, India, and South Africa, and probably North America, presented the same kind of resemblance as the mammals and birds of the corresponding Arctogæal Fauna do now But then there is no information respecting the Reptiles and Amphibians of the corresponding epoch in Austrocolumbia and Australia, so that it is impossible to say whether, in Triassic times, the Arctogæal province was limited as it is now.

Outside the limits of the Arctogæal province, the materials for forming a judgment of the distribution of animals are altogether insufficient to enable us to draw any conclusion as to the existence, and still less as to the boundaries, of definite provinces of distribution in Palæozoic times. No remains of land animals have yet been discovered. The fresh-water fauna consists of Amphibians and Fishes, and we know nothing, or next to nothing of these in any part of the world except the Arctogæal province.

A good deal is known of the older Silurian fauna outside the boundaries of the present Arctogæal province, and within those of both the Austrocolumbian and Australasian provinces. With a generally similar *facies* the faunæ of these regions present clear differences. And, considering that the groups of animals which are represented are chiefly deep sea and pelagic forms, it is not wonderful that this similarity of facies should exist. The investigations of the 'Challenger' expedition show that such forms present a like similarity of facies, at the present day.

One of the most important facts which have been established under the head of Zoological Chronology, is, that in all parts of the world, the fauna of the later part of the Tertiary period, in any province of distribution, was made up of forms either identical with, or very similar to those now living in that area.

For example, the elephants, tigers, bears, bisons, and hippopotamuses of the later tertiary deposits of England are all closely allied to members of the existing Arctogæal

fauna; the great armadillos, anteaters, and platyrrhine apes of the caves of South America are as closely related to the existing Austrocolumbian fauna; and the fossil kangaroos, wombats and phalangers of the Australian tertiaries to those which now live in the Australasian province.

No remains of elephants occur in Australia, nor kangaroos in Austrocolumbia; nor anteaters and armadilles in Europe in tertiary deposits.

But as we go back in time from the Tertiary to the Secondary, this law no longer holds good. Most of the few terrestrial mammals of secondary age which have been discovered belong to Australasian and not to Arctogæal types, and the marine fauna resembles that of the existing Pacific more than it does that of the Atlantic area, but differs from both in the presence of numerous wholly extinct groups. It looks as if, in the latter part of the Cretaceous epoch, a great change in the limits of the then existing distributional area had taken place, and the types now characteristic of the Arctogæal province had invaded regions from which they had before been shut out. And the assumption of a process of a similar character appears to me to be the only rational explanation of the rapid advent of types absent in the palæozoic deposits known to us, in the earlier Secondary rocks.

Yet other results of first-rate importance have come out of the study of the chronological relations of fossil remains. Cuvier's investigations proved that the hiatuses between existing groups of ungulate mammals tend to be filled up by extinct forms. Later investigations have not only confirmed this conclusion, but have shown that, in several cases, an existing much modified form can be shown to have been preceded in time, in the same distributional area, by exactly such forms as it is necessary should have existed, if the much modified existing animal had proceeded by way of evolution from a simpler form.

For certain groups of animals, then, there is as much and as good evidence of their having been evolved by successive modification of a primitive form as the nature of

the case permits us to expect. But the groups in which there is evidence of such modifications during geologically recorded time, all belong to the most differentiated members of their classes. Lower forms, co-extensive in duration, exhibit no sign of having undergone any notable modification While the former are *mutable*, the latter are *persistent types* in relation to geological time.

Leaving the debateable question of the nature of *Eozoon* aside, the oldest fossiliferous rocks are the Cambrian. The scanty fauna therein preserved consists of forms which are neither *Protozoa* nor *Porifera*, nor even appertain to the lowest groups of their respective classes. There is no reason to believe that it gives a just notion of the contemporaneous fauna, nor is there any valid reason for the supposition that it represents the forms of animal life which were the first to make their appearance on our planet.

CHAPTER II.

THE PROTOZOA.

In its feeblest manifestations, the contractility of animals results in mere changes of the form of the body, as in the adult *Gregarinæ*; but, from the sluggish shortenings and lengthenings of the different diameters of the body which these creatures exhibit, all gradations are traceable, through those animals which push out and retract broad lobular processes, to those in which the contractile prolongations take the form of long and slender filaments. Whether thick or filamentous, such contractile processes are called "pseudopodia," when their movements are slow, irregular, and indefinite; "cilia" or "flagella," when they are rapid and occur rhythmically in a definite direction; but the two kinds of organs are essentially of the same nature. It will be convenient to distinguish those *Protozoa* which possess pseudopodia, as *myxopods*, and those which are provided with cilia or flagella, as *mastigopods*.

The *Protozoa* are divisible into a lower and a higher group. In the former—the Monera—no definite structure is discernible in the protoplasm of the body; in the latter —the Endoplastica—a certain portion of this substance (the so-called nucleus) is distinguishable from the rest;* and, very commonly, one or more "contractile vacuoles" are present. The name of *contractile vacuoles* is given to spaces in the protoplasm, which slowly become filled with a clear watery fluid, and, when they have attained a certain

* I adopt this distinction as a matter of temporary convenience, though I entertain great doubt whether it will stand the test of further investigation.

size, are suddenly obliterated by the coming together, on all sides, of the protoplasm in which they lie. This systolic and diastolic movement usually occurs at a fixed point in the protoplasm, at regular intervals, or rhythmically. But the vacuole has no proper wall, nor, in most cases, is any trace of it discernible at the end of the systole. Occasionally, the vacuole certainly communicates with the exterior, and there is some reason to think that such a communication may always exist. The function of these organs is entirely unknown, though it is an obvious conjecture that it may be respiratory or excretory.

The "nucleus" is a structure which is often wonderfully similar to the nucleus of a histological cell, but, as its identity with this is not fully made out, it may better be termed "endoplast." It is, usually, a rounded or oval body embedded in the protoplasm, and but slightly different therefrom in either its optical or chemical characters Generally it becomes more deeply stained by such colouring matters as hæmatoxylin or carmine, and resists the action of acetic acid better than the surrounding protoplasm

In a few *Protozoa* there are many endoplasts in the substance of the body, and the protoplasm shows some tendency to become partially differentiated into cells. But where, as in the higher *Infusoria*, the body presents a definite organisation, with permanently differentiated constituents, which may be properly termed tissues, these tissues do not result from the metamorphosis of cells, but originate from the protoplasm directly by changes of its physical and chemical characters.

Conjugation, followed by the development of germs, which are set free and assume the form of the parent, has been observed in several groups of the *Protozoa*, but it is not yet quite certain how far sexual distinctions are established among these animals.

I.—THE MONERA.

In these lowest forms of animals the entire living body consists of a particle of gelatinous protoplasm, in which no nucleus, contractile vacuole, or other definite structure is visible; and which, at most, presents a separation into an outer, more clear, and denser layer—the *ectosarc*; and an inner, more granular and fluid matter — the *endosarc*. The outer layer is the seat of active changes of form, whereby it is produced into pseudopodia, which attain a certain length and are then retracted, or are effaced by the development of others from adjacent parts of the body. These pseudopodia are sometimes broad short lobes, at others, elongated filaments. When lobate, the pseudopodia remain distinct from one another, their margins are clear and transparent, and the granules which they may contain plainly flow into their interior from the more fluid central part of the body. But, when they are filiform, they are very apt to run into one another, and give rise to networks, the constituent filaments of which, however, readily separate and regain their previous form; and, whether they do this or not, the surfaces of these pseudopodia are often beset by minute granules, which are in incessant motion—like those which are observable on the reticulations of the protoplasm of the cells in a *Tradescantia* hair.

The myxopod thus described moves about by means of its contractile pseudopodia, and takes the solid matters which serve as its food into all parts of its body by their aid; while the undigested exuvia of the food are rejected from all parts of the body in the same indiscriminate way. It is an organism which is devoid of any visible organs except pseudopodia; and, so far as is known at present, it multiplies by simple division.

The *Protamœba* (with lobate pseudopodia) and *Protogenes* (with filamentous pseudopodia) of Haeckel are *Monera* of this extremely simple character. In *Myxodictyum* (Haeckel) the pseudopodia of a number of such *Monera* run together,

and give rise to a complex network, or common *plasmodium*.

It is open to doubt, however, whether either *Protamœba*, *Protogenes*, or *Myxodictyum* is anything but one stage of a cycle of forms, which are more completely, though perhaps not yet wholly, represented by some other very interesting *Monera*, also described by Haeckel.

Thus, the genus *Vampyrella* is a myxopod with filamentous pseudopodia, a species of which infests one of the stalked Diatomaceæ, *Gomphonema*, feeding upon the soft parts of the frustules of its host, by inserting some of its pseudopodia through the raphe of the frustule, which it envelopes, and absorbing the contained protoplasm. Having thus provided itself with abundant nourishment, by creeping from frustule to frustule of the *Gomphonema*, it thrusts aside the last evacuated frustule from its peduncle, and, taking its place, draws in its pseudopodia, becomes spherical, and surrounds itself with a structureless cyst, enclosed in which it remains, perched upon the peduncle of the *Gomphonema*. Soon, its protoplasm undergoes division into four equal masses, and each of these becoming converted into a young *Vampyrella*, escapes from the cyst, and recommences the predatory life of its parent. In this case, the myxopod becomes encysted, and then undergoes fission into bodies, each of which passes directly into the form of the parent.

In another genus (*Myxastrum*) an additional complication is introduced; the myxopod becomes encysted, and then divides into many portions; each of these elongates, and surrounds itself with a delicate, fusiform, silicious case. Thus enclosed, the germs are set free by the bursting of the cyst; and, after a while, the contents of the silicious cases emerge, and pass at once into the myxopod state.

In other genera, not only does the myxopod become encysted, before it undergoes fissive multiplication, but the forms thus produced differ from the myxopod in being free-swimming organisms, propelled by a long vibratile filament or flagellum, like those flagellate *Infusoria* which

Fig. 1

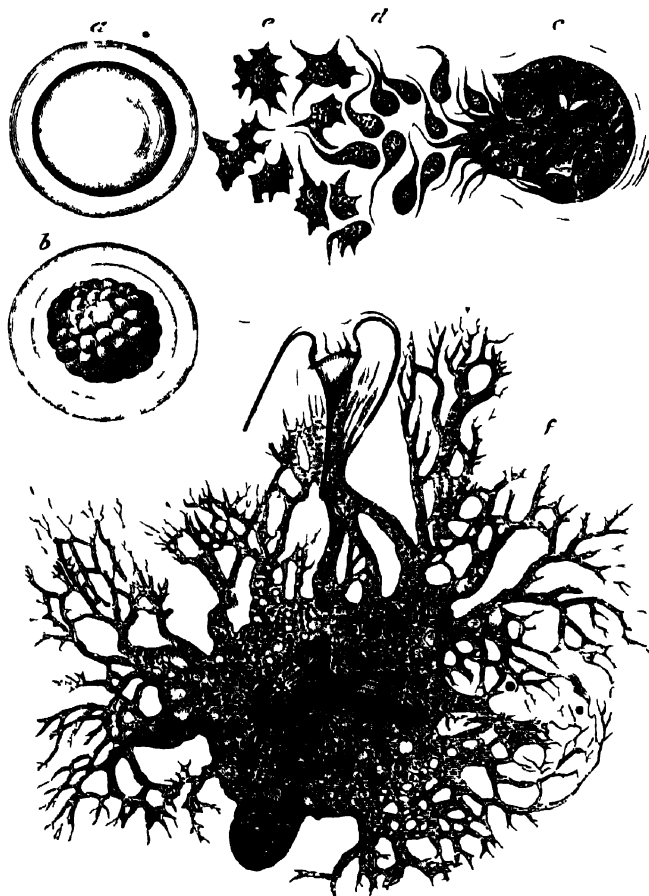


Fig. 1.—*Protomyxa aurantiaca* (Haeckel).—*a*, the still condition surrounded by a structureless cyst; *b*, encysted form, the protoplasm of which is dividing; *c*, the cyst bursting and giving exit to the bodies into which the protoplasm breaks up. There are at first 'monads,' *d*, each being provided with a flagelliform cilium, by means

of which it propels itself (*d*). After a time each monad retracts its cilium and resumes an Amœba-like form; (*e*) many of these coalesce and form a single plasmodium, which grows and feeds under the form *f*. The specimen figured contains a *Peridinium* (above), three *Dictyocystæ* (below), and two *Isthmiæ* (Diatomaceous plants) in the centre. (Haeckel, 'Studien über Moneren,' 1870.)

are termed "monads." After swimming about for a while, these mastigopods draw in their flagella, and become creeping myxopods. This cycle of forms is exhibited by the genus *Protomonas* of Haeckel. Lastly, in *Protomyxa* (Fig. 1) (Haeckel), there is an alternation of a mastigopod (*d*) with a myxopod form (*e*), as in *Protomonas*. But each myxopod does not usually become encysted alone. On the contrary, a certain number of the myxopods unite together, and become fused into an active plasmodium (*f*), which exhibits no trace of their primitive separation. The plasmodium becoming quiescent and spheroidal, surrounds itself with a structureless cyst (*a*), divides into numerous portions (*b*), which are converted into flagellate mastigopods, and these finally return to the myxopod condition (*c*, *d*, *e*). The cycle of life is here singularly similar to that presented by the *Myxomycetes*, which have hitherto been usually regarded as plants.

There is no means of knowing whether the cycle of forms presented by *Protomonas* and *Protomyxa* is complete, or whether some term of the series is still wanting, and considering how low down among plants the sexual process occurs, it seems quite possible that some corresponding sexual process yet waits to be discovered among the *Monera*. It is possible that the fusion of separate *Myxodictya* and *Protomyxæ* into a plasmodium may be a process of sexual conjugation. On the other hand, it may well be that these extremely simple organisms have not yet reached the stage of sexual differentiation.

The FORAMINIFERA.—Doubtless many *Monera* remain to be discovered, but they will probably be minute and inconspicuous organisms like the majority of those already described. The *Foraminifera*, on the other hand, are *Monera* of the *Protogenes* type, which, nevertheless, play and have played

an important part in the history of the globe, by reason of their power of fabricating skeletons or shells, which may be composed of horny (chitinous?) matter, or of carbonate of lime, secreted from the water in which they live, or may be fabricated by sticking together extraneous matters, such as particles of sand.

The first step from such an organism as *Protogenes* to the *Foraminifera* is seen in the *Lieberkühnia* of Claparède, where the pseudopodia are given off from only a small part of the surface of the body, the rest remaining naked and flexible.

In *Gromia* there is a similar restriction of the area from

Fig. 2.

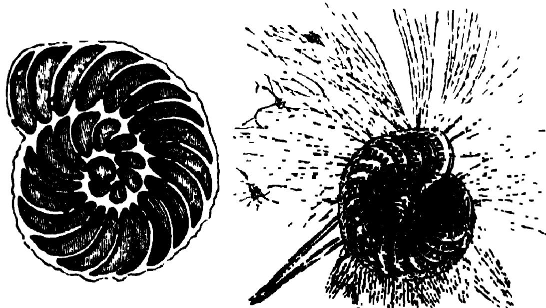


Fig. 2.—A *Rotalia*, with extended pseudopodia; with an enlarged sectional view of the chambered skeleton (after Schulze).

which pseudopodia proceed, but the rest of the body is invested by a case of a membranous substance. Let this case become hardened by the attachment of foreign bodies —as particles of sand, or fragments of shelly matter, as in the so-called arenaceous *Foraminifera*, —or let a deposit of calcareous salts take place in it, and the *Gromia* would be converted into a Foraminifer.

The infinitely diversified characters of the skeleton of the *Foraminifera* depend—firstly, upon the structure of the skeletal substance itself; and, secondly, upon the form of the protoplasmic body, which last, again, is largely depen-

dent upon the manner in which successive buds of protoplasm are developed from the parent mass, which, to begin with, is always simple in form and commonly globular

The substance of the calcareous skeleton itself, whatever be its form, is either perforated or imperforate. In the *Imperforata* (*Gromidæ*, *Lituitidæ*, *Miliolidæ*) the pseudopodia are protruded from only one end of the body, the rest of which is cut off from the exterior by the skeleton. In the *Perforata*, the substance of the shell is traversed by more or less delicate canals, filled with the protoplasm,

Fig. 3.

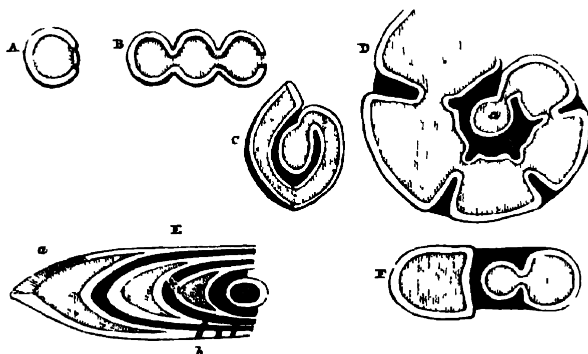


Fig 3 Diagrams of *Foraminifera.*—A, monothalamian; B, C, polythalamian; D, horizontal; E and F, vertical sections of helicoid form. In E, the chambers of each turn of the spiral overlap their predecessors and conceal them, as in the genus *Nummulites.*

which thus reaches the surface and gives off pseudopodia all over the body. Hence, while the hard parts of the *Imperforata* form a sort of exo-skeleton, those of the *Perforata* have rather the nature of an endo-skeleton.

The simplest skeletons are spherical or flask-shaped, and single-chambered. But complication arises by the addition of new chambers, which may form a linear series, or be coiled upon one another in various ways, or be irregularly aggregated. Moreover, the new chambers may overlap those

already formed in different degrees, and the interspaces between the walls of the chambers may be variously filled up by secondary deposition, until such large and apparently complicated bodies as the Nummulites are built up.

The *Foraminifera* are almost all marine animals, living in the sea, from the surface to great depths, sometimes free, and sometimes attached to other bodies.

The investigations of Major Owen, confirmed and extended by the recent work of H.M.S. 'Challenger,' have proved that such forms as *Globigerina*, *Pulvinularia*, and *Orbulina* constantly occur at the surface of all temperate and tropical seas, and, together with the *Radiolaria* and the Diatomaceous plants which accompany them, form an important ingredient in the food of pelagic animals, such as the *Salpæ*.

It is no less certain that at all depths down to 2400 fathoms or thereabouts, *Globigerinæ* in all stages of growth and containing more or less protoplasmic matter are found at the bottom, mixed with the cases of the surface Diatoms and the skeletons of *Radiolaria*. The proportion of *Globigerinæ*, *Orbulinæ*, and *Pulvinulariæ* in the deep-sea mud increases with the depth, until, at depths beyond 1000 fathoms, the sea-bottom is composed of a fine chalky ooze made up of little more than the remains of these *Foraminifera* and their associated Diatoms and *Radiolaria*.

It may be regarded as certain, therefore, that some of the chalky ooze arises from the precipitation to the bottom of the skeletons of dead *Globigerinæ*, *Pulvinulariæ* and *Orbulinæ*, and it may be that the whole has this origin. On the other hand, it may be that a greater or smaller proportion of these *Foraminifera* really live at the bottom, as their congeners are known to do at less depths.

It has been said that the condition of the surface waters and sea-bottom which has just been described, obtains in all temperate and hot seas; or, speaking roughly, for 55° on either side of the equator. Towards the northern and southern limits of this zone the *Foraminifera* diminish, while *Radiolaria* remain and *Diatomaceæ* increase in proportion, so that, in the circumpolar areas north and south of 60° in

each hemisphere, the surface organisms are chiefly such as have silicious skeletons. In accordance with this condition of the surface life, the ooze covering the sea-bottom in these regions is no longer calcareous but silicious, being composed of the cases of Diatoms and the skeletons of *Radiolaria* often largely mixed with ice, drifted mud, stones, gravel, and boulders.

If we suppose the globe to be uniformly covered with an ocean 1000 fathoms deep, the solid land forming its bottom would be out of reach of rain, waves, and other agents of degradation and no sedimentary deposits would be formed. But if *Foraminifera* and Diatoms, following the same laws of distribution as at present obtain, were introduced into this ocean, the fine rain of their silicious and calcareous hard parts would commence; and a circumpolar cap of silicious deposit would begin to make its appearance in the north and in the south; while the intermediate zone would be covered with *Globigerina* ooze, containing a comparatively small proportion of silicious matter. The thickness of the calcareo-silicious and silicious beds thus formed would be limited only by time and the depth of the ocean. These strata, once accumulated, would be liable to all those influences of percolating moisture and subterranean heat, which are known to suffice to convert silicious matters into opal, or quartzite, and calcareous matters into the various forms of limestone and marble. And such metamorphic agencies might more or less completely obliterate the traces of their primitive structure.

But yet other changes might be effected. At the present day, in the Gulf of Mexico, off the Agulhas bank, and elsewhere, at no great depths (100 to 300 fathoms) the Foraminiferal mud is undergoing a metamorphosis of another character. The chambers of the *Foraminifera* become filled by a green silicate of iron and alumina, which penetrates into even their finest tubuli, and takes exquisite and almost indestructible casts of their interior. The calcareous matter is then dissolved away, and the casts are left, constituting a fine dark sand, which, when

crushed, leaves a greenish mark, and is known as 'Greensand.'

Moreover, the researches of the 'Challenger' have shown, that in great areas of the Atlantic and Pacific oceans over which the sea has a depth exceeding 2400 fathoms—areas in some cases of many thousand square miles in superficies—the bottom is covered not by *Globigerina* ooze, but by a fine red clay, which is also a silicate of iron and alumina. In this clay no remains of *Globigerina* or other calcareous organisms are found; but where these great depths gradually pass into shallower water, they make their appearance in a fragmentary condition—gradually becoming more and more perfect as the depth diminishes to 2400 fathoms or thereabouts.

Nevertheless the *Globigerinæ* and other *Foraminifera* abound at the surface over these areas as they do elsewhere, and their remains must be rained down upon it. Why they disappear, and what relation the red clay mud has to them, is a problem not yet satisfactorily solved. It has been suggested that they are dissolved and that the red clay is merely the insoluble residue, left after the calcareous portion of their skeletons has disappeared. In this case the red clay, like the *Globigerina* ooze, the silicious mud, and the greensand, will be an indirect product of living action.

Metamorphic processes operating upon clay, however, may convert it into slate; and thus, all the fundamental minerals of which rock masses are composed may have formed part of living organisms, though no trace of their origin may be discernible in them in their final state.

Palæontology lends much support to the view that what is here suggested as a theoretically possible origin of much of the superficial crust of the globe, may have been its actual origin.

The nummulitic limestones of the Eocene epoch cover an enormous area of central and southern Europe, North Africa, West Asia and India. And their chief mass is made up of the more or less metamorphosed remains of *Foraminifera*.

The beds of chalk which underlie the nummulitic limestones, and occupy a still greater area, are essentially identical with the *Globigerina* ooze, the species of *Globigerina* found in it being indistinguishable from those now living. The remains of *Foraminifera* have been detected in the limestones of all epochs as far as the Silurian, and Ehrenberg discovered that an old Silurian greensand, near St. Petersburg, is composed of casts of *Foraminifera* just such as are now being formed in the Gulf of Mexico. And if the *Eozoon canadense* be, as it appears to be, nothing but an encrusting form of Foraminifer, the existence of these organisms is carried back to an epoch far beyond that at which any other evidence of life has yet been found. So that it is possible that, as Wyville Thomson has suggested, the enormously thick "azoic" slaty and other rocks, which constitute the Laurentian and Cambrian formations, may be to a great extent the metamorphosed products of Foraminiferal life.

Hence the words of Linnæus may be literally true—

> "Petrefacta non a calce, sed calx a petrefactis. Sic lapides ab animalibus, nec vice versa. Sic rupes saxei non primævi, sed temporis filiæ."

And there may be no part of the common rocks, which enter into the earth's crust, which has not passed through a living organism at one time or another.

II.—THE ENDOPLASTICA.

1. The RADIOLARIA.—Most species of the genus *Actinophrys* or "sun-animalcule," which is common in ponds, are simply free swimming myxopods with stiffish pseudopodia, which radiate from all sides of the globular body. The substance of the latter presents one or more "contractile spaces" or "vacuoles," which, rhythmically, become distended with water, and are then obliterated by the contraction of the surrounding protoplasm. But in the *Actinophrys* (or more properly *Actinosphærium*) *Eichhornii* (Fig. 4), the central part of the protoplasm is distinguished from the rest by

containing a number of endoplasts. It thus leads to the *Radiolaria* (*Polycistina* of Ehrenberg), the simplest forms of

Fig. 4.

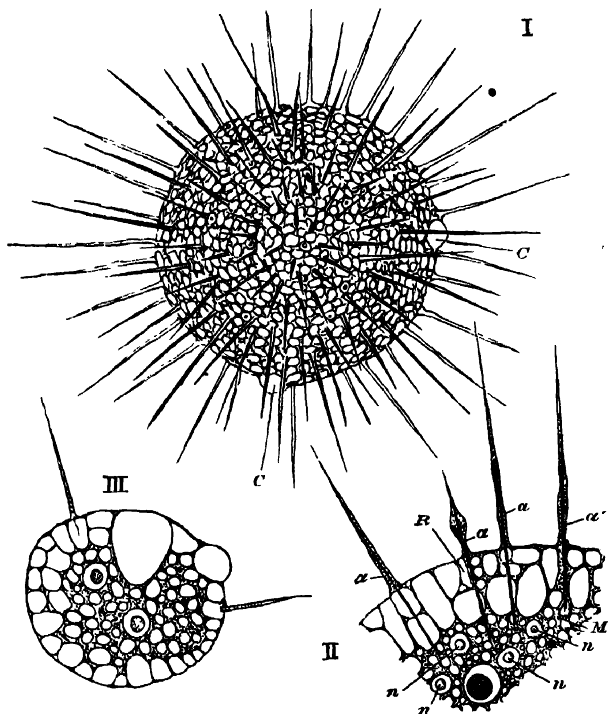


Fig. 4.—*Actinosphærium Eichhornii* (after Hertwig and Lesser, 'Ueber Rhizopoden,' Schulze's Archiv, 1876).
I.—The entire animal; *c*, *c*, contractile vacuoles.
II.—Part of the periphery much magnified; *a*, *a*, *a*, pseudopodia with stiff axial substance; *n*, nuclei or endoplasts.
III.—A very young *Actinosphærium*, with only two nuclei and two pseudopodia, much magnified.

which consist essentially of a myxopod, provided with filamentous, radiating, and often anastomosing, pseudo-

podia. The centre of the body is occupied by a capsule filled with protoplasm; this sometimes contains only an oil-

Fig 5

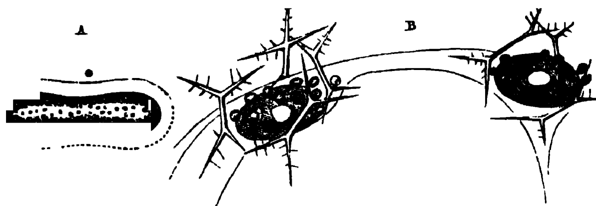


Fig. 5.—*Sphærozoum punctatum.*—A, a mass of the natural size; B, two of the oval central sacs with the coloured vesicles and spicula which lie in the investing protoplasm, magnified.

Fig. 6.

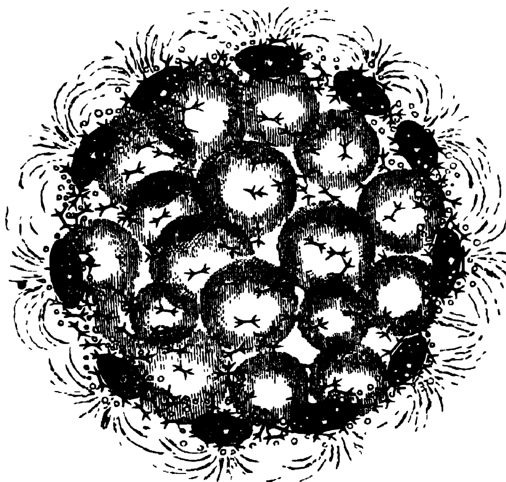


Fig. 6.—*Sphærozoum ovodimare* (after Haeckel), magnified.

globule, at others cells or nuclei, and crystalline bodies. In the layer of protoplasm from which the pseudopodia proceed,

cellæform bodies of a bright yellow colour, which have been found to contain starch, are usually developed,* and this layer also gives rise to a skeleton of a horny, or, more usually, silicious character, which may have the form of detached spicula, or of coarticulated rods, or of networks, or of plates of silicious matter, often of the most exquisite delicacy and beauty. Most of the *Radiolaria* are simple, solitary, and microscopical in size; but some, such as *Collosphæra* and *Sphærozoum* (Figs. 5 and 6), are formed of aggregates of such simple forms, and float, as visible gelatinous masses, at the surface of the sea, which is the habitation of the great majority of the *Radiolaria*.

The manner of multiplication and the development of the *Radiolaria* have not yet been thoroughly worked out. Cienkowsky, however, has observed, in *Collosphæra*, that the protoplasm contained in the central capsule breaks up into numerous rounded masses. The several capsules which are associated together in the compound Radiolarian then become isolated, by the dissolution of the protoplasm which invested and connected them, and finally burst, giving exit to the rounded bodies; which, while yet within the capsules, were observed to be in active motion. The germs (for such they appear to be) thus set free are 0·008 mm. long, ovate, and carry two flagelliform cilia at their narrow ends; so that they are 'monads.' Each has in its interior a crystalline rod and a few minute oil-globules. The further development of these mastigopods has not yet been traced; but if, as is probable, they pass into young *Radiolaria* (which, according to Haeckel, possess no capsule, but resemble *Actinosphæria*), the *Radiolaria*, as members of the *Endoplastica*, would typify *Protomonas* among the *Monera*. Neither conjugation nor fission has been observed among the ordinary *Radiolaria*, but both these processes take place in *Actinosphærium*; and, considering the resemblance of the young *Radiolaria* to *Actino-*

* Even after the death of the Radiolarian, these yellow cells are said by Cienkowsky to thrive and multiply, and the possibility that they may be parasites must be borne in mind.

sphærium, it seems probable that conjugation and fission will yet be discovered among them.

Actinosphærium has been observed to undergo multiplication, by division of its central substance into a certain number of spheroids, and every spheroid becomes enclosed in a silicious case. After a period of rest, a young *Actinosphærium* emerges from each of these cysts.

The marine *Radiolaria* all inhabit the superficial stratum of the sea, and must fabricate their skeletons at the expense of the infinitesimally small proportion of silex which is dissolved in sea-water; but when they die, these skeletons sink to the bottom, and there accumulate, together with the *Foraminifera*, in warm and temperate regions; and with the cases of the diatomaceous plants, which abound at the surface, along with the *Radiolaria*, all over the globe (see p. 85). The late investigations of Archer and others have demonstrated the existence of a considerable number of fresh-water *Radiolaria*.

Extensive masses of tertiary rock, such as that which is found at Oran, and that which occurs at Bissex Hill, in Barbadoes, are very largely made up of exquisitely preserved skeletons of *Radiolaria*. But, though there can be little doubt that *Radiolaria* abounded in the cretaceous sea, none are found in the chalk, their silicious skeletons having probably been dissolved and redeposited as flint.

2. The PROTOPLASTA.—The proper *Amœbæ* have broad and ovate pseudopodia, and resemble *Protamœba* (p. 78) very closely; but they present an advance upon its structure by exhibiting a distinct endoplast (nucleus) and a contractile vacuole. In *Arcella*, there are many such nuclei. They thus stand in somewhat the same relation to *Protamœba* as *Actinophrys* does to *Protogenes*.

Moreover, there are *Amœbæ* in which the power of throwing out pseudopodia is confined to one region of the body; and others, as *Arcella*, in which a shell is formed over the rest of the body. In other *Amœbæ*, as *A. radiosa*, the pseudopodia are few, narrow, and but little mobile. But the *Amœbæ* present no such diversity of skeletal develop-

ment as the *Foraminifera* do. They multiply by division, and in some cases—*e.g.*, *A. sphærococcus* of Haeckel—become encysted before they divide.

Amœbæ (the "proteus animalcules" of the older writers) are not uncommon, and sometimes are very abundant, in fresh waters; they also occur in damp earth and in the sea, but there is much doubt whether many of them are to be regarded as independent organisms, or whether they are not rather stages in the development of other animals or even of plants, such as *Myxomycetes*. Leaving out the contractile vacuole, the resemblance of an *Amœba* in its structure, manner of moving, and even of feeding, to a colourless corpuscle of the blood of one of the higher animals is particularly noteworthy.*

3. The GREGARINIDÆ are very closely allied to the *Amœbæ*, but, in the cycle of forms through which they pass, they curiously resemble *Myxastrum*. In form, they are spheroidal or elongated oval bodies, sometimes divided by constrictions into segments. Occasionally, one end of the body is produced into a sort of rostrum, which may be armed with recurved horny spines.

In the ordinary *Gregarinæ*, the body presents a denser cortical layer (ectosarc) and a more fluid inner substance (endosarc), in which last the endoplast (nucleus) is imbedded. The presence of contractility is manifested merely by slow changes of form, and nutrition appears to be effected by the imbibition of the fluid nutriment, prepared by the organs of the animals in which the *Gregarinæ* are parasitic. There is no contractile vacuole.

The *Gregarinæ* have a peculiar mode of multiplication, sometimes preceded by a process which resembles conjugation. A single *Gregarina* (or two which have become applied together) surrounds itself with a structureless cyst. The nucleus disappears, and the protoplasm breaks up (in a manner very similar to that in which the protoplasm of a sporangium of *Mucor* divides into spores) into small

* Contractile vacuoles have been observed in the colourless blood corpuscles of *Amphibia* under certain conditions.

bodies, each of which acquires a spindle-shaped case, and is known as a *pseudo-navicella*. On the bursting of the cyst these bodies are set free, and, when placed in favourable circumstances, the contained protoplasm escapes as a small active body like a *Protamœba*. M. E. van Beneden has recently discovered a very large *Gregarina* (*G. gigantea*), which inhabits the intestine of the lobster, and his careful

Fig. 7.

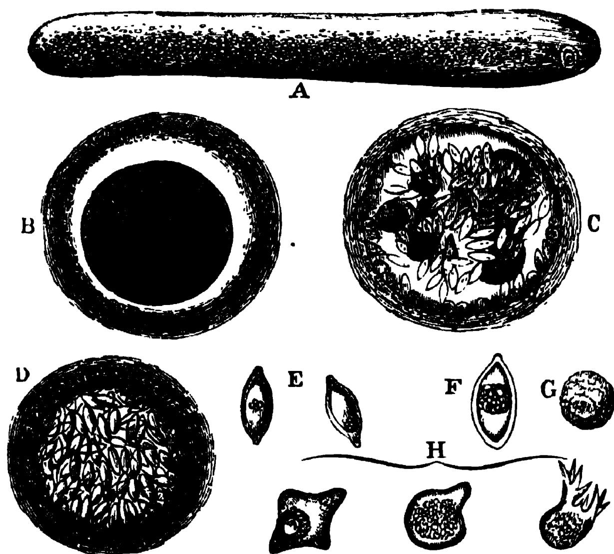


Fig. 7.—A, *Gregarina* of the earthworm (after Lieberkühn); B, encysted; C, D, contents divided into pseudo-navicellæ; E, F, free pseudo-navicellæ; G, H, free amœbiform contents of the latter.

investigation of its structure and development has yielded very interesting results.

Gregarina gigantea attains a length of two-thirds of an inch. It is long and slender, and tapers at one extremity, while the other is obtuse, rounded, and separated by a slight constriction from the rest of the body, which is cylindroidal.

The outer investment of the body is a thin structureless cuticle; beneath this lies a thick cortical layer (ectosarc), distinguished by its clearness and firmness from the semifluid central substance (endosarc), which contains many strongly refracting granules. In the centre of the body, the ellipsoid "nucleus," with its "nucleolus," fills up the whole cavity of the cortical layer, and thus divides the medullary substance into two portions. The body of this *Gregarina* may present longitudinal striations, arising from elevations of the inner surface of the cortical layer, which fit into depressions of the medullary substance; but these are inconstant. On the other hand, there are transverse striations which are constant, and which arise from a layer of what are apparently muscular fibrillæ, developed in a peripheral part of the cortical layer, immediately below the cuticle. The fibrillæ themselves are formed of elongated corpuscles joined end to end. A transverse partition separates the cephalic enlargement from the body, and the layer of muscular fibres only extends into the posterior part of the enlargement.

The embryos of *Gregarina gigantea*, when they leave their pseudo-navicellæ, are minute masses of protoplasm similar to *Protamœbæ*, and like them devoid of nucleus and contractile vacuole. They soon cease to show any change of form, and acquire a globular shape, the peripheral region of the body at the same time becoming clear. Next, two long processes bud out from this body; one is actively mobile, the other still. The former, detaching itself, assumes the appearance and exhibits the motions of a minute thread-worm, whence M. van Beneden terms it a *pseudo-filaria*. The enlargement at one end becomes apparent, the pseudo-filaria passes into a quiescent state, and the "nucleolus" makes its appearance in its interior. Around this a clear layer is differentiated, giving rise to the "nucleus," and the pseudo-filaria passes into the condition of the adult *Gregarina gigantea*.

4. The CATALLACTA of Haeckel, represented by the genus *Magosphæra*, are, in one stage, myxopods with long pseudo-

podia, which, broad and lobe-like at the base, break up into fine filaments at their ends, and may therefore be said to be intermediate between those of *Protogenes* and those of *Protamœba*. The myxopod is provided with a distinct endoplast and a well-marked contractile space. When fully fed, it secretes a cyst and divides into a number of masses, each of which is converted into a conical body, with its base turned outwards and its apex inwards. These conical bodies are imbedded in a gelatinous matter, and thus cohere into a ball, from the centre of which they radiate. Each developes cilia around its base, and contains an endoplast and a contractile vacuole. After the complex globe thus formed has burst its envelope, it swims about for a while, like a *Volvox*. The several ciliated animalcules feed by taking in solid particles through the disk. They then separate, and, finally, retracting their cilia, become myxopods such as those with which the series started. *Magosphæra* is thus very nearly an endoplastic repetition of the moneran *Protomonas*—the mastigopod being provided with many small cilia, instead of with a couple of large flagella. On the other hand, the *Catallacta* are closely allied to the next group, and, I am disposed to think, might well be included in it.

5. The INFUSORIA.—Excluding from the miscellaneous assemblage of heterogeneous forms, which have passed under this name, the *Desmidiæ*, *Diatomaceæ*, *Volvocineæ*, and *Vibrionidæ*, which are true plants, on the one hand; and the comparatively highly organised *Rotifera*, on the other; there remain three assemblages of minute organisms, which may be conveniently comprehended under the general title of Infusoria. These are—(*a*) the so-called "Monads," or *Infusoria flagellata*; (*b*) the *Acinetæ*, or *Infusoria tentaculifera*; and (*c*) the *Infusoria ciliata*.

(*a*.) The FLAGELLATA.—These are characterised by possessing only one or two long whip-like cilia, sometimes (when more than one are present) situated at the same end of the body, sometimes far apart. The body very generally exhibits an endoplast and a contractile vacuole. There is

no permanently open oral aperture, but there is an oral region, into which the food is forced, and, passing into the endosarc, remains for some time surrounded by a globule of contemporaneously ingested water—a so-called "food vacuole." Professor H. James Clark, who has recently carefully studied the *Flagellata*, points out that, in *Bicosœca* and *Codonœca*, a fixed monadiform body is enclosed within a structureless and transparent calyx. In *Codosiga* a similar transparent substance rises up round the base of the flagellum, like a collar. In *Salpingœca* the collar around the base of the flagellum is combined with a calycine investment for the whole animal. In *Anthophysa*, there are two motor organs—the one a stout and comparatively stiff flagellum, which moves by occasional jerks, and the other a very delicate cilium, which is in constant vibratory motion.

The discrepancy between the two kinds of locomotive organs attains its maximum in *Anisonema*, which presents interesting points of resemblance to *Noctiluca*.

Multiplication by longitudinal fission was observed in *Codosiga* and *Anthophysa*, and probably occurs in the other genera. In *Codosiga* the flagellum is retracted before fission takes place, but the body does not become encysted; in *Anthophysa* the body assumes a spheroidal form, and is surrounded by a structureless cyst, before division occurs.

Conjugation has not been directly observed among most of the *Infusoria flagellata*, nor do any of them exhibit a structure analogous to the endoplastule of the *Ciliata*.

Messrs. Dallinger and Drysdale have recently worked out the life history of several flagellate "Monads," which occur in putrefying infusions of fish. They show that these *Flagellata* not only present various modes of agamic multiplication by fission, preceded or not by encystment, but that they conjugate, and that the compound body which results (the equivalent of the zygospore in plants) becomes encysted. Sooner or later, the contents of the cyst become divided either into comparatively large or excessively minute bodies, which enlarge and gradually take on the form of the parent.

The careful investigations of these authors lead them to conclude that, while the adult forms are destroyed at from 71°-80° C., the excessively minute sporules which have been mentioned, and which may have a diameter of less than $\frac{1}{200000}$ of an inch, may be heated to 148° C. without the destruction of their vitality.

In *Euglena viridis* (which, however, may be a plant) Stein * has observed a division of the "nucleus" to take place, whereby it becomes converted into separate masses, some of which acquire an ovate or fusiform shape, surrounding themselves with a dense coat, while others become thin-walled sacs, full of minute granules, each of which is provided with a single cilium. The ultimate fate of these bodies has not been traced.

A careful study of the singular genus *Noctiluca*, led me, in 1855, to assign it a place among the *Infusoria*, and recent investigations have conclusively proved that it is one of the *Flagellata*.

The spheroidal body of *Noctiluca miliaris* (Fig. 8) is about one-eightieth of an inch in diameter, and, like a peach, presents a meridional groove, at one end of which the mouth is situated. A long and slender, transversely striated tentacle overhangs the mouth, on one side of which a hard-toothed ridge projects. Close to one end of this is a vibratile cilium. A funnel-shaped depression leads into a central mass of protoplasm, connected by fine radiating bands with a layer of the same substance which lines the cuticular envelope of the body. There is no contractile vacuole, but an oval endoplast lies in the central protoplasm. Bodies which are ingested are lodged in vacuoles of the latter until they are digested.

According to the observations of Cienkowsky,† if a *Noctiluca* be injured, the body bursts and collapses, but the protoplasmic and other contents, together with the tentacle, form an irregular mass, the periphery of which eventually

* 'Organismus der Infusions-thiere,' ii. 56.

† "Ueber Noctiluca miliaris." (Schulze's 'Archiv für Mikroskop. Anatomie,' 1872.)

becomes vacuolated, enlarges, and secretes a new investment. But even a small portion of the protoplasm of a mutilated *Noctiluca* is able to become a perfect animal. Under some conditions, the tentacle of a *Noctiluca* may be retracted into the body, and, at all times of the year, spheroidal *Noctilucæ*, devoid of flagellum, tooth, or meridional groove, but otherwise normal, are to be found. These last are probably to be regarded as encysted forms. Multiplication may take place in at least two ways. Fission may

Fig. 8.

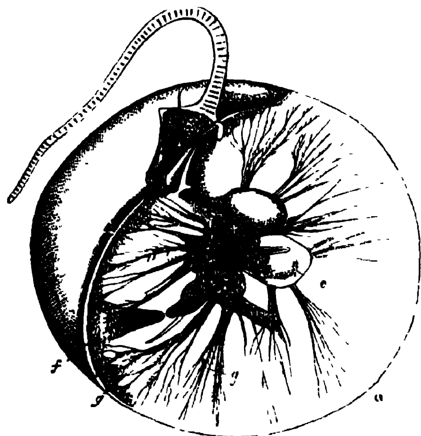


Fig. 8.—*Noctiluca miliaris.*—*e*, Gastric vacuole; *g*, radiating filaments; *f*. anal aperture. (?)

occur in the spheroidal forms, as well as in those possessed of a tentacle; it is inaugurated by the enlargement, constriction, and division of the endoplast. This process takes place more especially in the latter part of the year.

Another mode of asexual multiplication, which has a singular resemblance to the process of partial yelk division, occurs only in the spheroidal *Noctilucæ*. The endoplast disappears, and the protoplasm, accumulating on the inner

side of one region of the cuticle, divides first into two. then four, eight, sixteen, thirty-two, or more masses. the division of the protoplasm being accompanied by the elevation of the cuticle into protuberances, which, at first, correspond in number and dimensions with these division masses. When the division masses have become very numerous, each protrudes upon the surface, and is converted into a free monadiform germ, provided with an endoplast, a beak. and a long tentacle, which is hardly to be distinguished from a flagelliform cilium.

The process of conjugation has been directly observed. Two *Noctilucæ*, applying themselves by their oral surfaces, adhere closely together, and a bridge of protoplasm connecting the endoplasts of the two becomes apparent. The tentacula are thrown off, the two bodies gradually coalesce, and the endoplasts fuse into one. The whole process occupies five or six hours. Spheroidal or encysted *Noctilucæ* may conjugate in a similar manner. In this case, the regions nearest the endoplasts are those which become applied together. Whether this process is of a sexual nature, or not, is not clearly made out. Cienkowsky admits that it may hasten the process of multiplication by monadiform germs described above.

Noctiluca is extremely abundant in the superficial waters of the ocean, and is one of the most usual causes of the phosphorescence of the sea. The light is given out by the peripheral layer of protoplasm which lines the cuticle.

The *Peridineæ* (see Fig. 1, *f*) form another aberrant group of the *Flagellata*, which lead to the *Ciliata*. The body is enclosed in a hard case (sometimes produced into rays), which, at one part, presents a groove-like interruption, laying bare the contained protoplasm, in which lies an endoplast, and in some cases a contractile vacuole. One or more flagelliform cilia, and usually a wreath of short cilia, are protruded from the protoplasm, and serve as locomotive organs. The mouth is a depression, whence, in some cases, an œsophageal canal is continued and terminates abruptly in the semi-fluid central substance of the body, the food-particles being lodged in

vacuoles formed at its extremity, as in the *Ciliata*. No other mode of multiplication than that by fission has yet been observed in the *Peridineæ*; but this fission is sometimes preceded by the enclosure of the animal in an elongated crescent-shaped cyst.

(*b*.) The TENTACULIFERA.—The *Acinetæ* (Fig. 9, D, E, F, G) have no oral aperture of the ordinary kind, but filiform processes or tentacula, which are usually slender, simple, and more or less rigid, radiate from the surface of the body

Fig. 9.

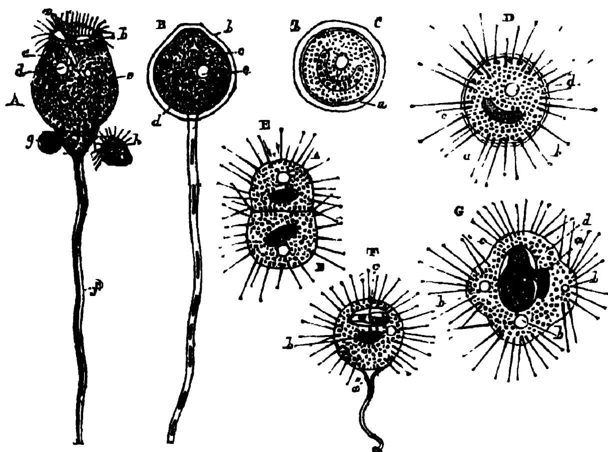


Fig. 9.—A, *Vorticella*, active; B, C, encysted; D, E, F, G, *Acineta* (after Stein).

generally, or from one or more regions of that surface. At first sight, these tentacula resemble the radiating pseudopodia of *Actinophrys*, but, on closer inspection, they are seen to have a different character. Each, in fact, is a delicate tube, presenting a structureless external wall, with a semi-fluid granular axis, and usually ends in a slight enlargement or knob. It may be slowly pushed out or retracted, or diversely bent. But, instead of playing the part of mere

prehensile organs, these tentacles act, in addition, as suckers; the *Acineta* applying one or more of these organs to the body of its prey*—usually some other species of Infusorium,—when the substance of the latter travels along the interior of the sucker into the body of the *Acineta*. Solid food is not ingested through these tentacles, so that the *Acinetæ* cannot be fed with indigo or carmine. In the interior of the body there is an endoplast† with one or more contractile vacuoles, and it may be either fixed by a stalk or free.

The *Acinetæ* multiply by several methods. One of these is simple longitudinal fission, which appears to be rare among them. Another method consists in the development of ciliated embryos in the interior of the body. These embryos result from the separation of a portion of the endoplast, and its conversion into a globular or oval germ, which, in some species, is wholly covered with vibratile

* Stein ('Der Organismus der Infusionsthiere,' i. 76) thus describes the method by which an *Acineta* seizes its prey: "If an Infusorium swims within reach of the *Acineta*, the nearest tentacles are swiftly thrown towards it, and, at the same time, often become much elongated, bent, or irregularly twisted about. The knob-like ends of these tentacles, which come into immediate contact with the surface of the entangled prey, spread out into disks, and adhere fixedly to it. When many of the tentacles have thus attached themselves, the imprisoned animal is no longer able to escape, its movements become slower, and at length cease. Those tentacles which have fixed themselves most firmly shorten and thicken, and draw the prey nearer to the body . . . Suddenly, as soon as the sucking disk has bored through the cuticula of the prey, a very rapid stream, indicated by the fatty particles which it carries, sets along the axis of the tentacle, and, at its base, pours into the neighbouring part of the body of the *Acineta*. . . . The cause of the movement is unknown. It is not accompanied by any discernible movement of the walls of the tentacle."

† No endoplastule, such as exists in other *Infusoria*, has been observed as yet in the *Acinetæ*. Under some circumstances, the *Acinetæ* draw in their radiating processes, and surround themselves with a structureless cyst; but this process does not appear to have any relation to either mode of multiplication.

In *Acineta mystacina* and *Podophrya fixa*, a peculiar mode of multiplication by division occurs. At the free end of the body a portion becomes constricted off, together with part of the endoplast, from the remaining stalked part. The tentacula are drawn in, and the segment becoming elongated, developes cilia over its whole surface and swims away.

cilia, while, in others, the cilia are confined to a zone around the middle of the embryo. The germ makes its escape by bursting through the body wall of its parent. After a short existence (sometimes limited to a few minutes) in the condition of a free swimming animalcule, provided with an endoplast and a contractile vacuole, but devoid of a mouth, the characteristic knobbed radiating processes make their appearance, the cilia vanish, and the animal passes into the *Acineta* state.

The *Acinetæ* have frequently been observed to conjugate, the separate individuals becoming completely fused into one, and their endoplasts coalescing into the single endoplast of the resultant *Acineta*; but it is not certainly made out, whether this process has, or has not, anything to do with the process of the development of ciliated embryos just described.

(*c.*) The CILIATA.—The characteristic feature of the *Ciliata* is, that the outer surface of the body is provided with numerous vibratile cilia, which are the organs of prehension and locomotion. According to the distribution of the cilia, Stein has divided them into the *Holotricha*, in which the cilia are scattered over the whole body, and are of one kind; the *Heterotricha*, in which the widely diffused cilia are of different kinds, some larger and some smaller; the *Hypotricha*, in which the cilia are confined to the under or oral side of the body; and the *Peritricha*, in which they form a zone round the body. The great majority of these animals are asymmetrical.

In the simplest and smallest *Ciliata*, the body resembles that of one of the *Flagellata* in being differentiated merely into an ectosarc and endosarc, with an endoplast and a contractile vacuole. In most, if not all cases, however, there is not only an oral region, through which the ingestion of food takes places, but an œsophageal depression leads from this into the endosarc; and it may be doubted whether, even in the simplest *Ciliata*, there is not an anal area through which the undigested parts of the food are thrown out.

The genus *Colpoda*, which is very common in infusions of hay, is a good example of this low form of ciliated Infusorium. It has somewhat the form of a bean flattened on one side, and moves actively about by means of numerous cilia, the longest of which are situated at the anterior end of the body. At the posterior end is the contractile vacuole, while a large endoplast lies in the middle, as Stein originally discovered. *Colpoda* frequently become quiescent, retract their cilia, and surround themselves with a structureless cyst. Each encysted *Colpoda* then divides into two, four, or more portions, which assume the adult form and escape from the cysts to resume an active existence.

Allman has described the encystment of a Vorticellidan, followed by division of the nucleus into many germs, without any antecedent process of conjugation; and Everts has observed that the progeny of an encysted *Vorticella* take on the form of *Trichodina grandinella*. The *Trichodinæ* multiply by transverse divisions, and then grow into *Vorticellæ*.*

Encystment, whether followed or not by division, is very common among all the *Ciliata*, and a species of *Amphileptus* has been seen to swallow—or rather envelope—a stalked bell-animalcule (*Vorticella*), and then become encysted upon the stalk of its prey, just as *Vampyrella* becomes perched upon the stalk of the devoured *Gomphonema*.

In the higher *Ciliata*, the protoplasm of the body becomes directly differentiated into various structures, in the same way as has already been seen to be the case in *Gregarina gigantea*, but to a much greater degree.

Thus, in the *Peritricha*, of which the bell-animalcules, or *Vorticellæ* (Fig. 9, A, B, C), are the commonest examples, the oral region presents a depression, the vestibule (Fig. 9, *a*), from which a permanent œsophageal canal leads into the soft and semi-fluid endosarc, where it terminates abruptly; and immediately beneath the mouth, in the vestibule, there is an anal region which gives exit to the refuse of digestion, but presents an opening only when fæcal matters are passing

* Allman, 'Presidential Address to the Linnean Society,' 1875.

out. Except where the ciliated circlet, or rather spiral, is situated, the outer wall of the body gives rise to a relatively dense *cuticula*, and not unfrequently secretes a transparent cup or case, foreshadowing the theca of hydrozoal polypes. Moreover, in the permanently fixed *Vorticellæ*, the stalk of attachment may present a central muscular fibre (Fig. 9, *f*), by the sudden contraction of which the body is retracted, the stalk being at the same time thrown into a spiral. In the

Fig. 10.

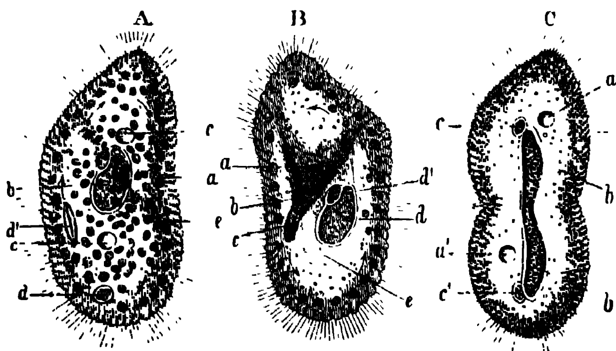


Fig. 10.—*Paramœcium bursaria* (after Stein).—A, the animal viewed from the dorsal side; *a*, cortical layer of the body; *b*, endoplast; *c*, contractile space; *d d'*, matters taken in as food; *e*, chlorophyll granules.

B, The animal viewed from the ventral side: *a*, depression leading to *b*, mouth; *c*, gullet; *d*, endoplast; *d'*, endoplastule; *e*, central protoplasm. In both these figures the arrows indicate the direction of the circulation.

C, *Paramœcium* dividing transversely; *a a'*, contractile spaces; *b b*, endoplast dividing; *c c'*, endoplastules.

holotrichous *Paramœcium* (Fig. 10) beneath the thin superficial transparent cuticle from which the cilia proceed, there is a very distinct cortical layer, fibrillated in a direction perpendicular to the surface, and, in some species of this or other genera, as *Strombidium* and *Polykricos* (Butschli), beset with minute rod-like bodies similarly disposed, which, under some circumstances, shoot out into long filaments, and have been

termed *trichocysts*. In *P. bursaria*, minute green granules of chlorophyll are dispersed through this layer, and Cohn demonstrated, in 1851, that these yield the same reactions as the chlorophyll grains of the Algæ. In *Balantidium*, *Nyctotherus*, *Spirostomum*, and many others, the cortical layer is divided by linear markings into bands, which there is reason to believe are rudimentary muscular fibres.

In many *Ciliata*, the endosarc appears to be almost fluid. The food, which is driven into the mouth and down the œsophagus by the constant action of the cilia, accumulates at the bottom of the œsophagus; and then, with the water which surrounds it, is passed, at intervals, with a sort of jerk, into the endosarc, where it lies, close to the end of the œsophagus, as a food vacuole, for a short time. But it soon begins to move, and, along with other such vacuoles formed before and after it, circulates in a definite course up one side of the body and down the other, between the cortical layer and the endoplast. This movement is particularly free and unrestricted in *Balantidium*; in *Paramœcium*, the tract through which the food vacuoles move is more definitely limited,* while, in *Nyctotherus*, it appears to be confined to a part of the body between the end of the gullet and the anal region, which, in this Infusorium, is seated at one end of the body. In fact, the finely granular endosarc of *Nyctotherus* so limits the passage of the food vacuoles, that the tract along which they pass might properly be described as a rudimentary intestinal canal.

The oral cavity is usually ciliated: sometimes, as in *Chilodon*, it has a chitinous armature, which becomes somewhat complicated in *Ervilia* (*Dysteria* †) and the *Didinium* described by Balbiani.

Torquatella (Lankester) has a plicated membrane around the mouth in the place of cilia.

The contractile vacuoles attain their greatest complexity

* In *Paramœcium bursaria*, Cohn observed that the circulation was completed in 1½ to 2 minutes, which gives a rate of rotation of $\frac{1}{9000}$ to $\frac{1}{12000}$th of an inch in a second.

† Huxley, "On Dysteria." ('Quarterly Journal of Microscop. Science,' 1857.)

in the *Paramœcia*, in which there are two—one towards each end of the body. They are lodged in the cortical layer, and, in diastole, a portion of their outer periphery is bounded only by the cuticle, through which it is very probable that they communicate with the exterior. When the systole takes place, a number of fine canals, which radiate from each vacuole, are seen to become distended with clear watery fluid. These canals are constant in their position, and some of them may be traced nearly as far as the mouth; so that the canals and vacuoles form a permanent water-vascular system. The endoplast is finely granular, like the substance of the endosarc. It is frequently said to be enveloped in a distinct membrane, but I am disposed to think that this is always a product of reagents. Attached to one part of it there is very generally (but not in the *Vorticellæ*) a small oval or rounded body, the so-called "nucleolus" or *endoplastule*. The endoplast is commonly said to be imbedded in the cortical layer, but this is certainly not the case in *Colpoda*, *Paramœcium*, *Balantidium*, or *Nyctotherus*.

The outermost, or cuticular, layer of a large portion of the body becomes hardened and forms a sort of shell, in many of the free *Infusoria*. In the free marine *Dictyocystida* and *Codonellida* of Haeckel, the body has a bell-shaped envelope, which in the *Dictyocystida* (see Fig. 1,) is strengthened by a silicious skeleton like that of a Radiolarian. In both genera the circular lip which surrounds the oral end is provided with numerous long flagelliform cilia.*

Most of the *Ciliata*, while in full activity, multiply by division; this is generally effected by the formation of a more or less transverse constriction, whereby the body becomes divided into two parts, which separate, each developing those structures which are needed for its completion. The endoplast, however, always elongates and divides, one portion going along with each product of fission. Neither budding nor longitudinal fission occurs among the free *Infusoria*, the appearances which have been regarded

* Haeckel, 'Zur Morphologie der Infusorien,' 1873.

as evidence of these processes being due to the opposite operation of conjugation. M. Balbiani,* its discoverer, thus describes this process of conjugation in *Paramæcium bursaria*:—

"The *Paramæcia* assemble in great numbers either towards the bottom or on the sides of the vessel in which they are contained. They then conjugate in pairs, their anterior ends being closely united; and they may remain in this state for five or six days or more. During this period, the nucleus and nucleolus become transformed into sexual organs.

"The nucleolus is changed into an oval capsule, marked superficially by longitudinal striæ. Sooner or later, it usually becomes divided into two or four portions, which grow independently, and form many separate capsules. About the time of separation, each of these is found to be a capsule containing a bundle of curved rods (*baguettes*), enlarged in the middle, and thinner at the ends.

"The nucleus also becomes enlarged, and gives rise—in a manner not clearly explained—to small spherical bodies analogous to ovules.

"It is usually about the fifth or sixth day after conjugation that the first germs appear, as little rounded bodies, formed of a membrane which is rendered visible by acetic acid, and of greyish pale homogeneous or almost imperceptibly granular contents, in which, as yet, neither nucleus nor contractile vacuole is distinguishable. It is only later that these organs appear. The observations of Stein and of F. Cohn have shown how these embryos leave the body of the mother under the form of *Acinetæ*, provided with knobbed tentacles and true suckers, by means of which they remain for some time adherent to her, and nourish themselves from her substance. But their investigations have not disclosed the ultimate fate of the young.

"I have been able to follow them for a long period after their detachment from the maternal organism; and I have

* Balbiani, "Note relative à l'Existence d'une Génération Sexuelle chez les Infusoires." ('Journal de la Physiologie,' tome i., 1858.)

been able to assure myself that, after having lost their tentacles, becoming clothed with vibratile cilia, and acquiring a mouth, which makes its appearance as a longitudinal groove, they return definitely to the parental form, developing in their interior the green granules which are characteristic of this *Paramœcium*, without undergoing any more extensive metamorphosis."

In Figs. 19–22 of Plate IV., which accompanies his paper, Balbiani figures all the stages by which the acinetiform embryo becomes a *Paramœcium.*

So far as the fact of conjugation, the changes in the "nucleolus," and the development of filaments in it, with the subsequent detachment, by division, of masses from the "nucleus" are concerned, these statements have not been modified by M. Balbiani, while they are fully confirmed by the observations made by himself, Claparède and Lachman, Stein, Kölliker, and others, in *Paramœcium bursaria, P. aurelia,* and other ciliated *Infusoria.*

In the closely allied *Paramœcium aurelia*, the occurrence of the various stages of conjugation, conversion of the "nucleolus" into bundles of spermatozoa, and subsequent division of the "nucleus" is also established by the coincident testimony of Balbiani and Stein. Balbiani affirms that, in this species, the clear globular bodies which result from the division of the "nucleus" pass out of the body without undergoing any further modification, and he considers them to be ovules. Stein also admits that he has never seen acinetiform embryos in this species.

But, as it would seem, on the strength of these negative observations in *Paramœcium aurelia*, Balbiani, in his later publications, asserts that the "acinetiform embryos" observed not only in *Paramœcium*, but in *Stylonychia, Stentor,* and many other ciliated *Infusoria*, are not embryos at all, but parasitic *Acinetæ;* and he makes this assertion without explicitly withdrawing the statement given above of his own observation of the passage of the acinetiform embryo of *Paramœcium bursaria* into the parental form. Engelmann and Stein, on the other hand, hold by Balbiani's

original doctrine, and give strong reasons for so doing. Among the most forcible analogical arguments are those afforded by the process of sexual reproduction observed by Stein in the peritrichous *Infusoria*.

In the *Peritricha* (*Vorticellidæ, Ophrydidæ, Trichodidæ*) conjugation takes place by the complete and permanent fusion of two individuals, which are sometimes of equal dimensions; though, in other cases, one is much smaller than the other, and, while it is in course of absorption, looks like a bud, and was formerly taken for such (Fig. 9, A, *g, h*). The small individuals usually take their origin from a group of small stalked *Vorticellæ*, which are produced by the repeated longitudinal division of a *Vorticella* of the ordinary size. The result of the conjugative act is that the "nuclei" of the two individuals, either before or after their coalescence, break up into a number of segments. The segments may remain separate or coalesce into a single mass, called by Stein, *placenta*. In the former case, some of the segments become germ masses, while the others reunite to form a new "nucleus;" in the latter, the placenta throws out a number of germ masses, and then assumes the form of an ordinary "nucleus." The germ masses give off portions of their substance, including part of their "nucleus," and these become converted into ciliated embryos, which escape by a special opening. Knobbed tentacles, like those of the *Acinetæ*, have not been observed in the embryos of the *Peritricha*, nor has their development been traced out.

If the bodies regarded as acinetiform embryos of the *Ciliata* are really such, they may be taken to represent the myxopod stage of the *Catallacta*, and the relations of the *Acinetæ* to the *Ciliata* would appear to be that they are modifications of a common type, differing from the *Catallacta* in having tentacula instead of ordinary pseudopodia. In the *Acinetæ*, the tentaculate stage is the more permanent, the ciliated stage transitory; while, in the *Ciliata*, the ciliated stage is the more permanent, and the tentaculate stage transitory.

CHAPTER III.

THE PORIFERA AND THE CŒLENTERATA.

1. THE PORIFERA or SPONGIDA.—It has been seen that, in the *Protozoa*, the germ undergoes no process of division analogous to the "yelk division" of the higher animals, and to the corresponding process by which the embryo cell of every plant but the very lowest becomes converted into a cellular embryo. Consequently, there is no blastoderm; the body of the adult Protozoon is not resolvable into morphological units, or cells, more or less modified; and the alimentary cavity, when it exists, has no special lining. Moreover, the occurrence of sexual reproduction in most of the *Protozoa* is doubtful, and there is, at present, no evidence of the existence of male elements, in the form of filamentous spermatozoa, in any group but the *Infusoria*; and even here the real nature of these bodies is still a matter of doubt.

In all the *Metazoa*, the germ has the form of a nucleated cell. The first step in the process of development is the production of a blastoderm by the subdivision of that cell, and the cells of the blastoderm give rise to the histological elements of the adult body, With the exception of certain parasites, and the extremely modified males of a few species, all these animals possess a permanent alimentary cavity, lined by a special layer of cells. Sexual reproduction always occurs; and, very generally, though by no means invariably, the male element has the form of filiform spermatozoa.

The lowest term in the series of the *Metazoa* is undoubtedly represented by the *Porifera* or Sponges, which,

after oscillating between the vegetable and the animal kingdoms, have, in recent times, been recognised as animals by all who have sufficiently studied their structure and the manner in which their functions are performed.

But the place in the Animal Kingdom which is to be assigned to the sponges has been, and still is, a matter of debate. It is certain that an ordinary sponge is made up of an aggregation of corpuscles, some of which have all the characters of *Amœbæ*, while others are no less similar to Monads; and therefore, taking adult structure only into account, the comparison of a sponge to a sort of compound *Protozoon* is perfectly admissible, and in the absence of other evidence, would justify the location of the sponges among the *Protozoa*.

But, within the last few years, the development of the sponges has been carefully investigated; and, as in so many other cases, a knowledge of that process necessitates a reconsideration of the views suggested by adult structure.

The impregnated ovum undergoes regular division; a blastoderm is formed, consisting of two layers of cells—an epiblast and a hypoblast,—and the young animal has the form of a deep cup, the wall of which is composed of two layers, an *ectoderm* and an *endoderm*, which proceed respectively from the epiblast and hypoblast. The embryo sponge is, in fact, similar to the corresponding stage of a hydrozoon, and is totally unlike any known condition of a protozoon.

Beyond this early stage, however, the sponge embryo takes a line of its own, and its subsequent condition differs altogether from anything known among the *Cœlenterata*; all of which, on the other hand, present close and intimate resemblances in their further development, as in their adult structure.

It is not long since the only sponge of the structure and development of which we were accurately informed was the *Spongilla fluviatilis*, or fresh-water sponge, the subject of the elaborate researches of Lieberkühn and Carter. But, recently, a flood of light has been thrown

Fig. 11.

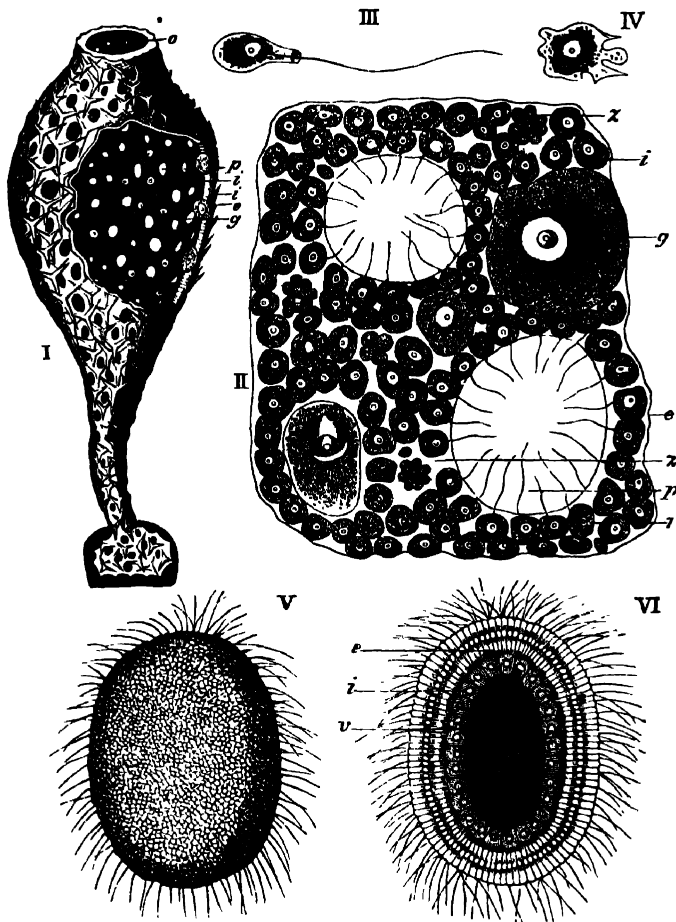


Fig. 11.—*Ascetta primordialis* (after Haeckel).
I., A mature *Ascetta*, part of one side of the body of which is removed ; *o*, the exhalent aperture ; *p*, inhalent pores in the wall of the body ;

i, endoderm; *e*, ectoderm; *g*, ova. The triradiate spicula are seen imbedded in the ectoderm.
II., A portion of the endoderm, with two pores (*p*); *i*, endodermal cells; those round the margins of the pores have their cilia directed inwards; *e*, ectodermal syncytium; *g*, ova; *z*, sperm cells.
III., A monadiform endodermal cell.
IV., An endodermal cell, with retracted cilium, and having the characters of an *Amœba*.
V., The ciliated embryo of *Ascetta mirabilis*.
VI., The same embryo in optical longitudinal section; *e*, epiblast; *i*, hypoblast; *v*, blastocœle.

upon the morphology and physiology of the marine sponges, particularly of those sponges with calcareous skeletons, which are termed *Calcispongiæ*, by Lieberkühn, Oscar Schmidt, and especially Haeckel. It has become clear that *Spongilla* is a somewhat aberrant form, and that the fundamental type of Poriferal organisation is to be sought among the *Calcispongiæ*. In the least complicated of the calcareous sponges, the body has the form of a cup, and is attached by its closed extremity. The open extremity is the *osculum*, and leads directly into the spacious *ventriculus*, or cavity of the cup. The comparatively thin wall of the cup is composed of two layers, readily distinguishable by their structure—the outer is the *ectoderm*, the inner the *endoderm*. The ectoderm is a transparent, slightly granular, gelatinous mass in which nuclei are scattered, but which, in the unaltered state, shows no trace of the primitive distinctness of the cells which contain these nuclei, and is therefore termed by Haeckel a *syncytium*. It is elastic and contractile, and sometimes exhibits an approach to fibrillation.

The endoderm, on the contrary, is composed of a layer of very distinct cells, each of which contains a nucleus and one or more contractile vacuoles, and is produced at its free extremity into a long solitary cilium or flagellum. Around the base of this, the transparent outer portion of the protoplasm of the cell is produced into an upstanding ridge like a collar, so that each cell has a wonderful resemblance to some forms of flagellate *Infusoria*. Microscopic apertures—the pores—scattered over the outer surface of the cup, lead into short passages which perforate the

ectoderm and endoderm, and thus place the ventriculus in communication with the exterior. The working of the flagella of the endodermic cells causes the water contained in the gastric cavity to flow out of the osculum; to make good this outflow, minute streams set in by the pores, which have consequently been called *inhalent*, while the osculum has been termed the *exhalent* aperture. It is said, however, that the direction of these currents is not invariable; and it is certain that the pores are not constant, but that they may be temporarily or permanently closed, and new ones formed in other positions.

The skeleton of the calcareous sponges always consists of a multitude of separate spicula, composed of an animal substance, more or less strongly impregnated with carbonate of lime, which is deposited in concentric layers around a central axis, formed by the animal basis. This skeleton is developed exclusively in the ectoderm, and is not supported by any framework of fibrous animal matter.

The calcareous sponges are frequently, if not always, hermaphrodite. The reproductive elements are ova and spermatozoa. There is some reason for assuming that the latter originate in metamorphosed cells of the endoderm, as they are found scattered between ordinary cells of the latter. The ova, on the other hand, occur sometimes between the cells of the endoderm, sometimes imbedded in the syncytium itself. But the question of the origin of the sexual elements in these and other animals, needs much further investigation. The spermatozoa are very delicate and have minute rod-like heads, with long flagella. The ova present the normal germinal vesicle and spot, but exhibit active amœboid movements.

Impregnation is effected, and the first stages of development take place, while the ova are still imbedded in the body of the sponge.

Metschnikoff* has recently described the development

* "Zur Entwickelungs-geschichte der Kalkschwämme." ('Zeitschr. für Wissenschaftliche Zoologie,' Bd. xxiv.) F. E. Schulze, so far as I follow Haeckel's account of his recent observations

of *Sycon ciliatum.* The ovum, after impregnation, becomes a morula, with a central cleavage cavity or *blastocœle.* But the blastomeres of the two halves of the morula take on different characters—those of the one half elongating and acquiring flagelliform cilia, while those of the opposite half remain globular and develope no cilia. The latter now coalesce into a syncytium, and develope spicula, while the layer of ciliated cells becomes invaginated within the syncytium. More usually, however, it appears that a gastrula is formed by invagination of the morula, the ectoderm of which has the structure of the endoderm of the adult, while the cells of the endoderm, or lining membrane of the gastric cavity, are devoid of cilia. The embryo quits the parent, propelled by the flagelliform cilia which cover the outer surface of the ectoderm. After a time, it fixes itself by the closed end; the flagella of the cells of the ectoderm are retracted, the cells themselves become flattened and coalesce so completely that their boundaries cease to be distinguishable, and the ectoderm passes into the condition of a syncytium. At the same time, the cells of the endoderm multiply, elongate, and take on the form which characterises them in the adult. In this state the young sponge is termed an *Ascula.* The transition to the final condition is effected by the development of the spicula in the syncytium and the separation of some of the constituent cells of the syncytium to form the inhalent pores.

In the simplest *Calcispongiæ*, forming the family to which Haeckel applies the name of *Ascones*, the wall of the ventriculus is thin, and the pores open directly into the ventricular cavity; but in another family, the *Leucones*, the syncytium becomes greatly thickened, and the pores are consequently prolonged into canals (which may be ramified

('Die Gastrula und die Eifurchung der Thiere,' p. 158), agrees with Metschnikoff as to the first stages of development, but differs in regard to subsequent stages. Haeckel withdraws his earlier account of the formation of the gastrula by delamination, or splitting of the walls of an oval shut *planula*-sac into two layers, and the subsequent opening of the planula at one end.

and anastomose), connecting the ventriculus with the exterior. The endodermic cells, which in these, as in the *Ascones*, at first form a continuous layer, are eventually restricted to the canals, or even to local dilatations of these canals—the so-called "ciliated chambers."

The same relative disproportion of the ectoderm, with the consequent development of passages which traverse the mass of the sponge, and are provided at intervals with ciliated chambers, is found in the silicious sponges, in which the spicula, if they possess any, are formed by a deposit of silex; and in which, as a rule, the sponge corpuscles are supported by a more or less complete skeleton of a tough animal substance, termed *keratose*.

Halisarca, however, is devoid both of skeleton and spicula, and the minute structure of the curious boring sponges—the *Clionæ*—has yet to be elucidated.

Haliphysema and *Gastrophysema*, of Haeckel, appear to be sponges which get no further than the *Gastrula* condition, and thus form a connecting link between the Sponges and the *Hydrozoa*.

The fresh-water sponge (*Spongilla*) has been studied with extreme care by Lieberkühn, and the following account, based upon the investigations of that author, is given for the use of the student to whom *Spongilla fluvialis* is likely to be the most readily accessible of the sponges.

The fresh-water sponge grows on the banks of docks, canals, rivers, and on floating timber, in the form of thick encrusting masses, which usually have a green colour, and require a constant supply of fresh water for their healthy maintenance. The surface presents irregular conical eminences perforated at their summit like small volcanic craters, and from these exhalent funnels, which answer to the *oscula* of the *Calcispongiæ*, currents of the water are continually flowing. Careful examination of the surface of the *Spongilla* between the exhalent craters, shows that it is formed by a delicate membranous expansion, separating which from the deeper substance of the *Spongilla* are a number of irregular cavities. In some cases, these run into one great water-

chamber. The superficial chambers, or chamber, communicate with the exterior by pores, which perforate the membranous expansion, are similar to those in the outer surface of the ventricular wall of a simple calcareous sponge, and subserve the same inhalent function. On their inner face, or floor, the superficial chambers exhibit the apertures of innumerable canals, which traverse the deep substance of the *Spongilla* in all directions, and, sooner or later, unite into passages which lead directly into the cavities of the exhalent craters. Dilatations of the canals occur at intervals, and are lined by the characteristic monadiform endodermic cells, which are restricted to the walls of these ciliated chambers. It is by the working of the cilia of these cells that currents of water are made continually to enter by the inhalent pores and to pass out by the exhalent craters. The whole fabric is supported and strengthened by a skeleton, which consists, in the first place, of bands and filaments of keratose, and, secondly, of silicious spicula, the majority of which resemble needles pointed at each end, and contain a fine central canal filled with an unsilicified substance. The individuality of these animals is so little marked that two *Spongillæ*, when brought into contact, before long fuse into one; while they may divide spontaneously, or be separated artificially into different portions, each of which will maintain an independent existence.

A process analogous to the formation of cysts, which is so common among the *Protozoa*, takes place in the deeper substance of the body, especially in the autumn. A number of adjacent sponge corpuscles, losing their granular appearance, become filled with clear strongly refracting granules, the nucleus ceasing to be visible. The sponge corpuscles which surround these become closely applied together, and secrete coats of keratose, which fuse with those of the adjacent corpuscles. In the interior of each a singular silicious spiculum is formed, consisting of two toothed disks, like cogged wheels, united by an axis. As this "*amphidiscus*" enlarges, the protoplasm of the cor-

puscle disappears, and at length nothing is left but the envelope of keratose, with the imbedded amphidisks, disposed perpendicularly to its surface. At one point of the spheroidal envelope, a small opening is left, and the so-called "seed" of the *Spongilla* is complete. It remains throughout the winter unchanged; but, with the return of warmth, the sponge corpuscles enclosed within the coat of the "seed," or more properly cyst, slowly escape through the pore, become perforated by inhalent and exhalent apertures and canals, and develope the characteristic spicula of a young *Spongilla*.

This process of encystment, which may be regarded as a kind of budding, akin to propagation by bulbs among plants, has not been observed among marine sponges.

Sexual propagation takes place in the same way as in the *Calcispongiæ*, and the embryo passes through morula and planula stages. But the ciliated cells which form the outer wall of the latter, and constitute its locomotive apparatus, seem to vanish when the embryo fixes itself, and the body of the young *Fibrospongia* appears to be developed out of the inner cells, which, in the meanwhile, have become spiculigerous. However, the details of the mode of development of the *Fibrospongiæ* require further elucidation.

In both the marine and the fresh-water sponges the ingestion of solid matters—such as carmine and indigo—by the monadiform endodermic cells has been seen by several observers. According to Haeckel, the solid particles, which usually are taken in between the flagellum and the collar, may also be ingested at other parts of the surface of the endodermic cell. In the course of such experiments, also, granules of the pigment may be found in the ectoderm, but whether they enter it directly, or secondarily from the endoderm is unknown. Sponges absorb oxygen, and give off carbonic acid with great rapidity; and the manner in which they render the water in which they live impure, and injurious to other organisms, suggests the elimination of nitrogenous waste matter.

The syncytium may contract as a whole, and is liable

to local contractions, as when the oscula or the pores shut or open. The contours of the cells of which it is composed are invisible in the fresh state, and hence it appears as a mere "sarcode" or transparent gelatinous contractile substance, in which nuclei and granules are imbedded here and there. But Lieberkühn has shown that, when the water in which *Spongilla* lives is heated to the point at which thermic coagulation of the protoplasm of the cells occurs, their boundaries at once become defined, and the cells commonly detach themselves from one another. The syncytium is therefore formed by the close union, and not by the actual fusion, of the cells of the body.

It is a very interesting fact that thread-cells, similar to those which are so abundant in the *Cœlenterata*, are said to occur in some sponges. Eimer* finds these structures in species of the *Renierinæ*. The thread-cells are scattered through both endoderm and ectoderm, and abound on the free surface of the former, where it limits the canals of the sponge, but do not occur on the outer surface of the ectoderm. The same observer states that he found partly digested remains of small crustaceans in the ventricular cavities and passages of both silicious and calcareous sponges.

The *Porifera* present three principal modifications—the *Myxospongiæ*, the *Calcispongiæ*, and the *Fibrospongiæ*, —the *Myxospongiæ* being altogether devoid of skeleton; the *Calcispongiæ* possessing calcareous spicula, but no fibrous keratose skeleton; and the *Fibrospongiæ* having a fibrous skeleton; and (usually) spicula of a silicious nature. To these it is probable that the *Clionidæ* must be added, as a fourth type, devoid of a fibrous skeleton, but possessing silicious spicula of a very peculiar kind, by the help of which they are able to burrow parasitically in the shells of mollusks. Finally, *Haliphysema* and *Gastrophysema* appear to be even simpler than the *Myxospongiæ*.

The division of the *Myxospongiæ* contains only the gela-

* "Nesseizellen und Saamen bei See-Schwämmen." ('Archiv für Mikroskropische Anatomie,' viii., 1872.)

tinous *Halisarca.* The *Calcispongiæ*, in addition to the two families of *Ascones* and *Leucones*, already referred to, include a third—the *Sycones*, which are essentially composite *Ascones.* The *Fibrospongiæ* present a great diversity of form and structure. They may have the form of flattened or globular masses, arborescent tree-like growths, flagellate expansions, or wide or deep cups. The sponge of commerce derives its value from the fact that its richly developed fibrous skeleton is devoid of spicula. On the other hand, in such sponges as *Hyalonema* and *Euplectella*, the silicious spicula attain a marvellous development and complexity of arrangement. In the latter genus, they form a fibrous network with regular polygonal meshes. These appear to be the representatives of the *Ventriculites*, which were so common in the seas of the Cretaceous epoch.

See page 121.

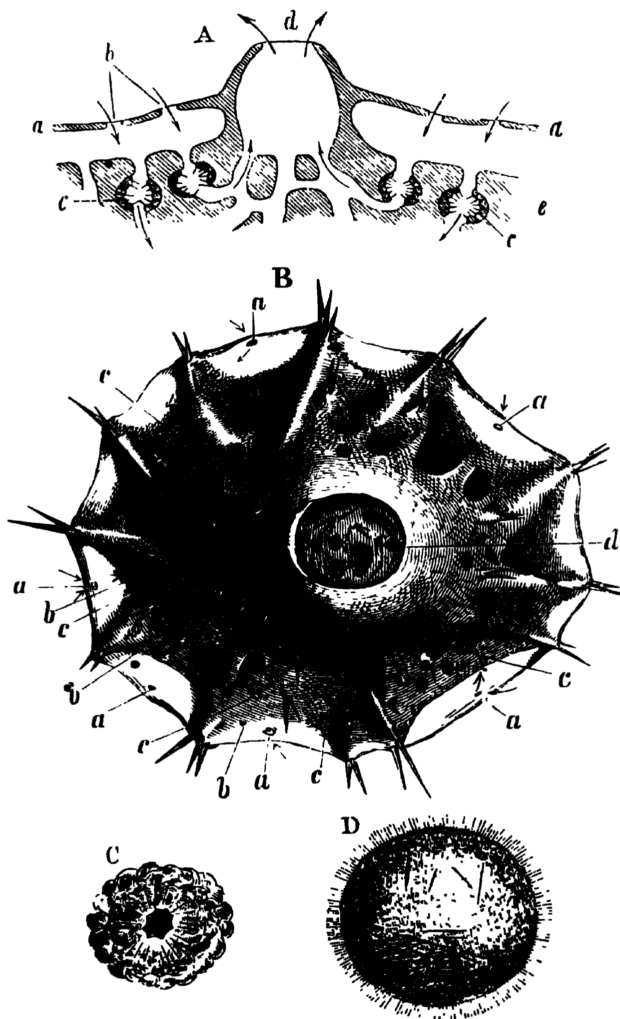
Fig. 12.—A, Hypothetical section of *Spongilla*: *a*, superficial layer; *b*, inhalent apertures; *c*, ciliated chambers; *d*, an exhalent aperture; *e*, deeper substance of the sponge. The arrows indicate the direction of the currents. B, a small *Spongilla* with a single exhalent aperture, seen from above (after Lieberkühn): *a*, inhalent apertures; *c*, ciliated chambers; *d*, exhalent aperture. C, a ciliated chamber. D, a free-swimming ciliated embryo.

Sponges abound in the waters of all seas, but *Spongilla* is the sole fresh-water form. *Clionidæ* existed in the Silurian epoch, but the most plentiful remains of sponges have been yielded by the chalk.

The Cœlenterata.—This group of the *Metazoa* contains those animals which are commonly known as Polypes, Jelly-fishes, or *Medusæ*, Sea anemones, and Corals. They exhibit two well-marked series of modifications, termed the *Hydrozoa* and the *Actinozoa.*

The Hydrozoa.—The fundamental element in the structure of this group is the *Hydranth*, or *Polypite.* This is essentially a sac having at one end an ingestive or oral opening, which leads into a digestive cavity. The wall of the sac is composed of two cellular membranes, the outer

Fig. 12.



of which is termed the *ectoderm*, and the inner the *endoderm*, the former having the morphological value of the epidermis

Fig. 13.

Fig. 13.—Diagrams illustrative of the mutual relations of the *Hydrozoa*:—
1. Hydra. 2. Sertularian. 3. Calycophoridan. 4. Physophoridan. 5. Lucernarian.
a. Ectoderm. *b*. Endoderm. *c*. The digestive and somatic cavity.
P. Tentacles. N. Nectocalyx. T. Cœnosarc. B. Hydrophyllium. C. Hydrotheca. S. Hydranth. G. Gonophore. A. Air Vesicle contained in F. Pneumatophore. *c*. Digestive and somatic cavity.
I., II., III., IV., represent the successive stages of development of a Medusiform gonophore.

of the higher animals, and the latter that of the epithelium of the alimentary canal.* Between these two layers, a

* "The body of every Hydrozoon is essentially a sac composed of two membranes, an external and an internal, which have been conveniently denominated by the terms *ectoderm* and *endoderm*. The cavity of the sac, which will be called the *somatic cavity*, contains a fluid, charged with nutritive matter in solution, and sometimes, if not always, with suspended solid particles, which perform the functions of the blood in animals of higher organisation, and may be termed the *somatic fluid*. . . . Notwithstanding the extreme variety of form exhibited by the Hydrozoa, and the multiplicity and complexity of the organs which some of them possess, they never lose the traces of this primitive simplicity of organisation; and it is but rarely that it is even disguised to any considerable extent. . . . This important and obvious structural peculiarity could hardly escape notice, and I find it to have been observed by Trembley, Baker and Laurent, Corda and Ecker in *Hydra*; by Rathke, in *Coryne*; by Frey and Leuckart, in *Lucernaria*; and it is given as a character of the hydroid polypes in general (*Hydræ*, *Corynidæ*, and *Sertularidæ*), in the second edition of Cuvier's 'Leçons.' I pointed it out as the general law of structure of the hydroid polypes, *Diphydæ* and *Physophoridæ*, in a paper[1] sent to the Linnean Society, from Australia, in 1847, but not read before that body till January, 1849; and I extended the generalisation to the whole of the *Hydrozoa*, in a 'Memoir on the Anatomy and Affinities of the *Medusæ*,' read before the Royal Society in June 1849.

"Professor Allman, in his valuable memoir 'On Cordylophora' (Phil. Trans. 1855), has adopted and confirmed this morphological law, introducing the convenient terms 'ectoderm' and 'endoderm,' to denote the inner and outer membranes, and Gegenbaur ('Beitrage zur naheren Kenntniss der Schwimmpolypen,' 1854, p. 42) has partially noticed its exemplification in *Apolemia* and *Rhizophysa*; but it seems singularly enough to have failed to attract the attention of other excellent German observers, to whose late important investigations I shall so often have occasion to advert. The peculiarity in the structure of the body walls of the *Hydrozoa* to which I have just referred, possesses a singular interest in its bearing upon the truth (for, with due limitation, it is a great truth) that there is a certain similarity between the adult states of the lower animals, and the embryonic conditions of those of higher organisation.

"For it is well known that, in a very early state, the germ, even of the highest animals, is a more or less complete sac, whose thin wall is divisible into two membranes, an inner and an outer; the latter turned towards the external world; the former, in relation with the nutritive liquid, the yelk. The inner layer, as Remak has more particularly shown, undergoes but little histological change, and throughout life remains more particularly devoted

[1] 'Observations upon the Anatomy of the Diphydæ, and the Unity of Organisation of the Diphydæ and Physophoridæ.' An abstract of this essay was published in the 'Proceedings of the Linnean Society' for 1849.

third layer—the *mesoderm*,—which represents the structures which lie between the epidermis and the epithelium in more complex animals, may be developed, and sometimes attains a great thickness, but it is a secondary and, in the lower *Hydrozoa*, inconspicuous production.

All the *Hydrozoa* are provided with *tentacula*. These are elongated and sometimes filiform organs of prehension, which are generally diverticula of both ectoderm and endoderm, but may be outgrowths of only one of them.

Thread-cells, or *nematocysts*, are very generally distributed through the tissues of the *Cœlenterata*. In its most perfect form, a nematocyst is an elastic, thick-walled sac, coiled up in the interior of which is a long filament, often serrated or provided with spines. The filament is hollow,

to the functions of alimentation, while the outer gives rise, by manifold differentiations of its tissue, to those complex structures which we know as integument, bones, muscles, nerves, and sensory apparatus, and which especially subserve the functions of relation. At the same time, the various organs are produced by a process of budding from one or other, or both, of these primary layers of the germ.

"Just so in the Hydrozoon: the ectoderm gives rise to the hard tegumentary tissues, to the more important masses of muscular fibres, and to those organs which we have every reason to believe are sensory, while the endoderm undergoes but very little modification. And every organ of a Hydrozoon is produced by budding from one, or other, or both of these primitive membranes; the ordinary case being that the new part commences its existence as a papillary process of both membranes, including, of course, a diverticulum of the somatic cavity.

"Thus there is a very real and genuine analogy between the adult Hydrozoon and the embryonic vertebrate animal; but I need hardly say it by no means justifies the assumption that the Hydrozoa are in any sense 'arrested developments' of higher organisms. All that can justly be affirmed is, that the Hydrozoon travels for a certain distance along the same great highway of development as the higher animal, before it turns off to follow the road which leads to its special destination."

In this passage of my work on the 'Oceanic Hydrozoa,' (1859,) I expanded the idea enunciated in the Memoir on the Medusæ here referred to, that, "the outer and inner membranes appear to bear the same physiological relation to one another as do the serous and mucous layers of the germ." The diagram (Fig. 13), exhibiting the relations of the different groups of the Hydrozoa, was published in the 'Medical Times and Gazette' in June, 1856.

and is continuous with the wall of the sac at its thicker or basal end, while its other, pointed, end is free. Very slight pressure causes the thread to be swiftly protruded, apparently by a process of evagination, and the nematocyst now appears as an empty sac, to one end of which a long fila-

Fig. 14.

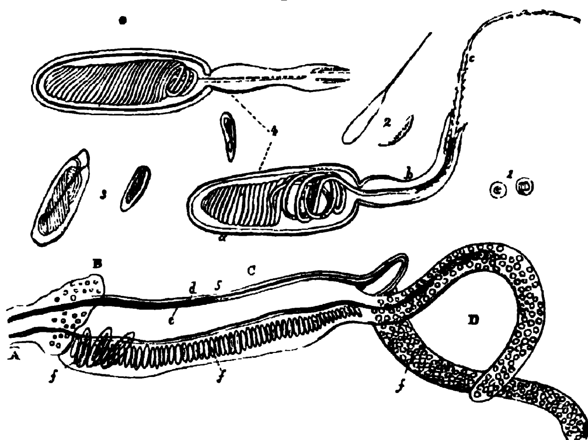


Fig. 14 —Sacculus of a tentacle with nematocysts of *Athorybia*. A, peduncle or stalk, and B, involucrum of the sacculus C; D, filaments; *d*, ectoderm; *e*, endoderm; *f*, nematocysts; 1, small nematocysts of the filaments and involucrum; 2, 3, larger nematocysts of the sac; 4, largest nematocysts.

ment, often provided with two or three spines near its base, is attached. Many of the *Cœlenterata*, and notably the *Physalia*, give rise to violent urtication when their tentacles come in contact with the human skin, whence it may be concluded that the nematocysts produce a like injurious effect upon the bodies of those animals which are seized and swallowed by the Polypes and Jelly-fishes.

As regards the existence of a nervous system in the *Hydrozoa*, very diverse opinions have been entertained, and it may be doubted if the problem has even yet received its final solution. I have already discussed Kleinenberg's

suggestion, that the branched prolongations of the inner ends of the cells of the ectoderm in *Hydra*, which end in the longitudinal fibres which lie between the ectoderm and the endoderm may be nerves in their earliest stage of differentiation. Haeckel describes a nervous system in *Glossocodon* and *Carmarina*. It consists of a circular band which lies on the inner side of the circular canal of the bell-shaped swimming organ of these *Medusæ*, and presents a ganglionic enlargement at the base of each of the lithocysts. Of these eight ganglia, the four which correspond to the openings of the four radial canals into the circular canal, are the larger. Each of these gives off four branches, one of which follows the course of the radial canal to the central polypite or manubrium; two others go to the adjacent tentacles, and the last to the lithocyst.*

There can be little doubt that the *lithocysts*, or sacs containing mineral particles, which are so frequently found in the Medusæ, are of the nature of auditory organs; while the masses of pigment, with imbedded refracting bodies, which often occur associated with the lithocysts, are doubtless rudimentary eyes.

The sexual reproductive elements are ova and spermatozoa —the ova being very often devoid of a vitelline membrane. The fully formed generative elements lie between the ectoderm and the endoderm of that part of the body wall in which they make their appearance. In *Hydractinia*, as has already been pointed out, the ova appear to be modified cells of the endoderm, and the spermatozoa modified cells of the ectoderm; but it remains to be seen how far this rule is of general application.

Usually, the region of the body in which the generative organs are produced undergoes a special modification before the reproductive elements make their appearance in it, giving rise to a peculiar organ, the *gonophore*. In its

* Haeckel, 'Beiträge zur Naturgeschichte der Hydromedusen.' The anatomical disposition of this nervous apparatus accords very well with the recent important observations of Mr. Romanes on the Locomotor system of Medusæ. (Proceedings of the Royal Society, December 1875.)

simplest condition the gonophore is a mere sac-like diverticulum, or outward process of the body wall. But, from this state, the gonophore presents every degree of complication, until it acquires the form of a bell-shaped body, called from its resemblance to a *Medusa* or jelly-fish, a *medusoid*.*

In its most complete form, the medusoid consists of a disk having the form of a shallow or deep cup (*nectocalyx*), from the centre of the concavity of which projects a sac termed the *manubrium*. The cavity of the sac is continued into that of sundry symmetrically disposed canals, most commonly four in number, which radiate from the centre of the disk to its circumference, where they open into a circular marginal canal. A membranous fold, the *velum*, which contains muscular fibres arranged concentrically to its free margin, is attached to the inner circumference of the mouth of the bell, and projects, like a shelf, into its interior. Lithocysts are usually developed on the margins of the bell, which may also give rise to tentacles. The manubrium, opening at its free end, may become functionally, as well as structurally, a hydranth, and may serve to feed the medusoid when it is detached from the *hydrosoma*, or body of the hydrozoon. However complex its structure may be, the medusoid commences as a simple bud-like outgrowth, which thickens at its free end; the central part of this thickening becomes the manubrium, while its periphery, splitting away from the manubrium, is converted into the disk (Fig. 13). A single prolongation of the somatic cavity is continued into the manubrium, while several, usually four, symmetrically arranged diverticula extend into the nectocalyx and become its radiating canals. The distal ends of these subsequently throw out lateral branches, which unite and give rise to the circular canal.

The lithocysts are usually, but not always, free and

* From the imperfection of our knowledge respecting the origin of many of the medusiform *Hydrozoa*, it is difficult to employ any terminology with strict consistency. If "medusoid" is restricted to what are known to be gonophores developed by gemmation, "medusa" may be employed, in a general sense, as the equivalent of the somewhat inconvenient vernacular term "jelly-fish."

prominent, and the one or many solid mineral bodies which they contain are enclosed in special envelopes. Their structure appears to be more complicated in the *Geryonidæ* than in other Medusæ. (Haeckel, *l. c.*)

In some of these medusoid gonophores, the reproductive elements are developed while the gonophore is still attached to the hydrosoma, and then they always make their appearance in the wall of the manubrium. But, in other cases, the medusoid becomes detached before the development of the reproductive elements, and, feeding itself, increases largely in size before the ova or spermatozoa appear. Sooner or latter, however, the reproductive organs are developed, either in the walls of the manubrial hydranth, or in those of the canals of the nectocalyx of the medusoid.

In an early stage of its existence, every hydrozoon is represented by a single hydranth, but, in the great majority of the *Hydrozoa*, new hydranths are developed from that first formed, by a process of gemmation or of fission. In the former case the bud is almost always an outgrowth or diverticulum of the ectoderm and endoderm, into which a prolongation of the cavity of the body extends. Sometimes the hydranth formed by gemmation becomes detached from the body; but, in many cases, the buds developed from the primary hydranth remain connected together by a common stem or *cœnosarc*, and thus give rise to a compound body, or *hydrosoma*.

In many *Hydrozoa*, the ectoderm gives rise to a hard cuticular coating, and in some of these (*Campanularidæ*, *Sertularidæ*, Fig. 13, 2), this cuticular investment, on the hydranth, takes the shape of a case or "cell"—the *hydrotheca*—into which the hydranth may be more or less completely retracted. In other *Hydrozoa*, protective coverings are afforded to the hydranths by the development of processes of the body wall, which become thick, variously-shaped, glassy lamellæ. These appendages are termed *hydrophyllia* (Fig. 13, 3).

Again, certain groups (the *Calycophoridæ* and most *Physophoridæ*) are provided with bell-shaped organs of

propulsion, produced by the metamorphosis of lateral buds of the *hydrosoma*. These *nectocalyces* have the structure of a medusoid, devoid of a manubrium. In others (*Physophoridæ*), one extremity of the hydrosoma is dilated, contains air enclosed within a sac formed by an involution of the ectoderm, and constitutes a float or *pneumatophore*; while in yet others (*Discophora*), the aboral end of the hydranth is dilated into a disk or *umbrella*, which is susceptible of rhythmical contractile movements, by which the body is propelled through the water. Thus, notwithstanding its different mode of development, it has a close resemblance to a medusoid. According to the existence or absence of these various appendages, and the manner in which they are disposed, the *Hydrozoa* are distinguishable into three groups—1, the *Hydrophora*; 2, the *Discophora*; 3, the *Siphonophora*.

1. The HYDROPHORA are, in all cases but that of *Hydra*, fixed ramified hydrosomes, on which many hydranths and gonophores are developed. The somatic cavity contained in the hydrosoma always retains a free communication with the gastric cavities of the hydranths. In other words, it is an *enterocœle*. The tentacula are either scattered over the hydranths (*Coryne*), or are arranged in one circle round the mouth (*Sertularia*); or in two circles, one close to the mouth, and one near the aboral end (*Tubularia*). Very generally—*e.g.*, in all *Sertularidæ*, *Campanularidæ*, and *Tubularidæ*—there is a hard, chitinous, cuticular skeleton, (*perisarc* of Allman,) which frequently gives rise to hydrothecæ, into which the hydranths can be retracted (Fig. 13, 2).

The gonophores present every variety, from simple saccular diverticula of the hydrosoma to free swimming medusoids. The inner margin of the bell in these medusoids is always produced into a velum, and otolithic sacs and eye-spots are very generally disposed at regular intervals around the circumference of the bell. The great majority of what were formerly termed the naked-eyed Medusæ (*Gymnophthalmata*) are merely the free-swimming

gonophores of the *Hydrophora*. Thus the medusoids known as *Sarsiadæ* are the free gonophores of the *Corynidæ*; the *Bougainvilleæ* and *Lizziæ* of the *Eudendridæ*; many *Oceanidæ* proceed from *Tubularidæ*; *Thaumantidæ* and *Æquoridæ* from *Campanularidæ*.

In some *Hydrophora* (*e.g.*, *Calycella*) the margins of the

Fig. 15.

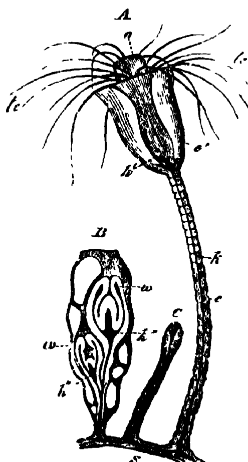


Fig. 15.—*Campanularia* (after Gegenbaur).—A, Hydranth; *e*, its peduncle; *e'*, hydrotheca; *o*, mouth; *te*, tentacles; *k'*, digestive cavity, continuous with the somatic cavity *k*, contained in the peduncle and in the creeping stem, S. B, gonangium containing two medusiform zooids or gonophores *w*; the somatic cavity *k''* is in connection with that of the creeping stem. C, Bud.

hydrotheca are prolonged into triangular processes, which serve as an operculum.

Certain *Plumularidæ* are provided with prominences of the hydrosoma surrounded by a chitinous investment, which is open at the extremity. The enclosed soft ectoderm usually contains many thread-cells, and has the power of throwing out contractile pseudopodial processes. These

have been termed *nematophores* by Mr. Busk.* In *Ophiodes* Hincks) they are tentaculiform.

It frequently happens that the gonophores are developed upon special stalks, each of which has essentially the structure of a mouthless hydranth. This is termed a *blastostyle*. In some blastostyles (Fig. 15), during the development of the buds of the gonophores, the ectoderm splits into two layers—an inner, which invests the central axis formed by the endoderm with the contained prolongation of the somatic cavity; and an outer, chiefly, if not wholly, chitinous layer. Into the interspace between these two, the budding gonophores project, and may emerge from the summit of the *gonangium*, thus formed, either to develope the reproductive elements, and shed them while still attached, or to be set at liberty as free medusoids (Fig. 16).

Fig. 16.

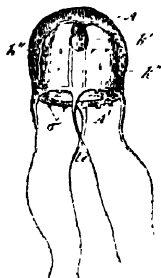


Fig. 16.—Medusiform zooid of *Campanularia* (after Gegenbaur). *A*, nectocalyx; *te*, tentacles; *σ*, lithocysts; *A'*, velum; *k'*, manubrium, enclosing the digestive cavity; *o*, mouth; *k''*, radial canals.

Allman † has shown that, in *Dicoryne conferta*, the gonophore contained in a gonangium, somewhat like that of *Laomedea*, is set free as a ciliated bitentaculate body, on the central axis of which the ova and spermatozoa are developed.

In the genus *Aglaophenia* (*Plumularidæ*), groups of gonangia are enclosed in a common receptacle (*corbula*, Allman), formed by the development and union of lateral processes (comparable in some respects to the hydrophyllia of the *Calycophoridæ*)

* They are described under the name of "clavate organs," and compared with the tentacles of *Diphydæ* in my Memoir on the "Affinities of the Medusæ." (Phil. Trans. 1849.)

† 'Monograph of the Gymnoblastic, or Tubularian Hydroids.' 1871, p. 31. In this beautifully illustrated and elaborate work, the student will find, not only a full account of the organisation of the group of which it treats, but much information respecting the *Hydrozoa* in general.

from that region of the hydrosoma, which bears the gonophores.

Some medusoids, such as *Sarsia prolifera* and *Willsia*, the hydroid stages of which are not at present certainly known, but which are probably coryniform, produce medusoids similar to themselves by budding. The buds may be developed either from the manubrium, or from the marginal canal of the nectocalyx, or from the bases of the tentacula, or even from their whole length.

Fig. 17.

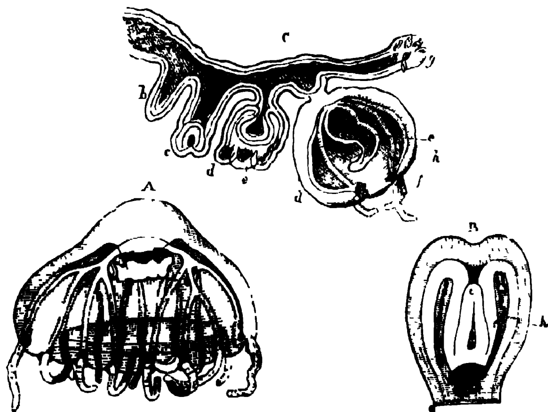


Fig. 17.—*Willsia, sp.*—A, the medusa, with budding stolons. B, one of the buds developed on a stolon; *h*, radial canal of the nectocalyx; *e*, manubrium. C, a stolon: *g*, its free end beset with nematocysts; *b*, *c*, *d*, budding medusoids; *f*, medusoid nearly ready to be detached; *e*, its manubrium; *d*, its nectocalyx; *h*, a radial canal.

In August, 1849, while in the North Pacific, off the Louisiade Archipelago, I took a species of *Willsia* (Fig. 17), in which stolons were developed at the bifurcation of each of the four principal radiating canals of the nectocalyx. Each stolon was terminated by a knobbed extremity containing many nematocysts (C, *g*), and gave rise, on one side, to a series of buds, of which those nearest the free end of the

stolon had acquired the form of complete medusoids. They had four unbranched radiating canals and four tentacles; but it is probable that they would assume the form of the parent stock after detachment.

In striking contrast with the complexity of these reproductive processes, the gonophore is represented, in *Hydra*, by a mere enlargement of the body wall, situated close to the bases of the tentacula, in the case of the testes, and nearer the attached end of the body in that of the ovary. The ovary developes a single ovum, which, as Kleinenberg has shown, undergoes division and invests itself with a chitinous coat while still attached to the body of the parent. This chitinous investment is more or less spinose, and is often confounded with an egg-shell. It obviously answers to the *perisarc* of a Tubularian, and its presence in the embryo of the *Hydra*, in which no perisarc is developed by the adult, suggests that *Hydra* may not represent the simplest primary condition of a Hydrophoran, but may be a reduced modification of a Tubularian.

2. The Discophora.—These "Medusæ" resemble the more perfect free medusoid gonophores of the *Hydrophora*, in so far as they consist of a hydranth or polypite attached to the centre of a gelatinous contractile swimming disk. But they differ from the medusoids of the *Hydrophora*, inasmuch as they are developed either directly from the impregnated ovum; or by gemmation from a Medusa which arises in this way; or by the transverse fission of the hydriform product of the development of the impregnated ovum.

In some of these (*e.g.*, *Carmarina, Polyxenia, Æginopsis, Trachynema*), the disk is similar to the nectocalyx of one of the medusoids of the *Hydrophora*; and, like it, is provided with a velum. But in the rest (*Lucernaria* and the *Steganophthalmata*) the disk is either devoid of a velum, or possesses only a rudiment of that structure, and is termed an *umbrella*. The edges of the umbrella are divided into lobes by marginal notches in which the lithocysts are lodged. Moreover in these, the mineral particles of the lithocysts

are numerous, and not enclosed in separate sacs. The lithocysts are often covered by hood-like processes of the umbrella, whence they have been termed "covered-eyed" or *Steganophthalmata.*

Lucernaria is fixed by the aboral side of its umbrella (Fig. 13, 5), by means of a longer or shorter peduncle. The umbrella is divided into eight lobes, at the extremities of each of which there is a group of short tentacles. The

Fig. 18.

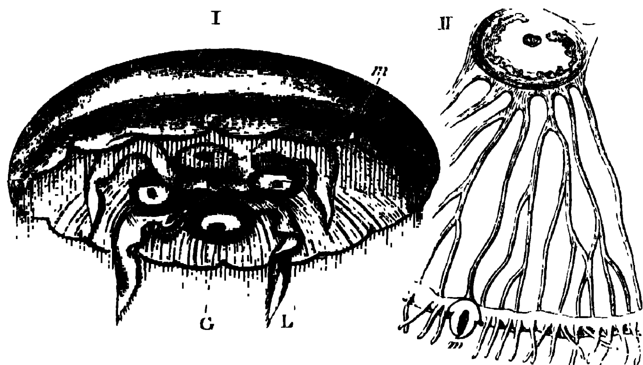


Fig. 18.—I. *Aurelia aurita.*—L, the prolonged angles of the mouth; G, genital chambers; *m*, lithocysts.
II. Under view of a segment of the disk, to show the arrangement of the radiating canals; the aperture of a genital chamber and the plaited genital membrane showing through its ventral wall; and a lithocyst with its protective hood (*m*).

hydranth stands up in the centre of the umbrella, and its cavity communicates with a central chamber, whence four wide chambers pass into the lobes. These chambers are separated by septa, the free central edges of which are beset with slender tentacles. The reproductive organs are double radiating series of thickenings of the oral wall of each chamber.*

* The relations of *Lucernaria* with the *Discophora*, were shown in my lectures, 'Medical Times and Gazette,' 1856. Keferstein, 'Un-

All the other *Discophora*, which are what are commonly known as "Jelly-fish," are free, and some attain a very large size. In the adult (Fig. 18) the umbrella is thick and divided by small marginal notches into as many (usually eight) lobes. At the bottom of each notch, often protected by special lobules, is an oval lithocyst, supported by a cylindrical peduncle, the cavity of which is in direct communication with one of the radiating canals of the umbrella (Fig. 28, IV.). This canal communicates with the exterior on the aboral side of the base of the peduncle.* The thick mesoderm of which the great mass of the umbrella consists is composed of a gelatinous connective tissue, in the meshes of which is a watery fluid, containing numerous nucleated cells which exhibit amœboid movements. On the oral face there is a broad zone of striped muscle, made up of fusiform fibres placed side by side. In *Aurelia aurita*, the angles of the four-sided hydranth are produced into long foliaceous lips, the margins of which are beset with minute solid tentacula (Fig. 18). The gastric cavity contained in the hydranth terminates, beneath the centre of the umbrella, in a somatic cavity which passes into four radially-disposed wide offshoots, or *genital sinuses*, the oral walls of which constitute the roof of the genital chambers (Fig. 18, II.). From their margins the narrow branching radial canals are given off. The peripheral ends of these unite when they reach the margin.

Each genital chamber is a recess, surrounded by a thick wall of the oral face of the umbrella, in the centre of

tersuchungen über niedere Seethiere' (1862), in his monograph on the genus, fully confirms this view, and Prof. H. J. Clark arrived independently at the same conclusion: "*Lucernaria* the Cœnotype of the *Acalephæ*" (Proceedings of the Boston Society of Natural History, 1862). The *Lucernaria* (*Carduella*, Allman) *cyathiformis* of Sars differs much from the ordinary *Lucernariæ*, especially in the position of the genital organs as longitudinal thickenings in the walls of the gastric cavity. See Allman, "On the Structure of *Carduella cyathiformis*" (Trans. Microscop. Society, viii.)

* The circular canal of the nectocalyx communicates with the exterior by apertures on the summits of papillose elevations in some medusoids.

which only a small aperture is left (Fig. 18, I. G). The roof of this cavity is the floor of the genital sinus; it is much plaited and folded, and the genital elements are developed in it. Its inner or endodermal wall is beset with small tentacular filaments (Fig. 28, III.). The ova or the spermatozoa

Fig. 19.

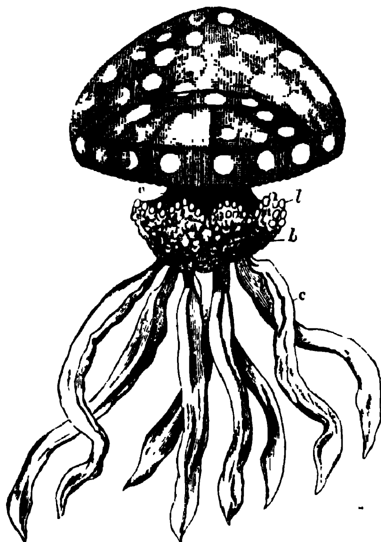


Fig. 19.—*Cephea ocellata* (?).—The entire animal: *a*, the umbrella; *b*, the ramifications of the brachia; *c*, the tentacles which terminate them; *o*, the pillars which suspend the brachiferous disk which forms the floor of the sub-umbrellar cavity; *l*, short clavate tentacles between the oral pores.

pass out of the apertures of the genital chambers, and the ova are received into small pouches or folds of the lips, and there undergo the preliminary stages of their development.

In the *Rhizostomidæ* (as was originally suggested by Von

Baer and has been proved by L. Agassiz and A. Brandt.*) the margins of the lips of the hydranth unite, leaving only a multitude of small apertures for the ingestion of food on the long arms, which represent prolongations of the lips of the hydranth (Figs. 19, 20, 21). The polystomatous condition thus brought about, by the subdivision of a primitively simple oral cavity, is obviously quite different in its nature from that which occurs in the *Porifera.*

Fig. 20.

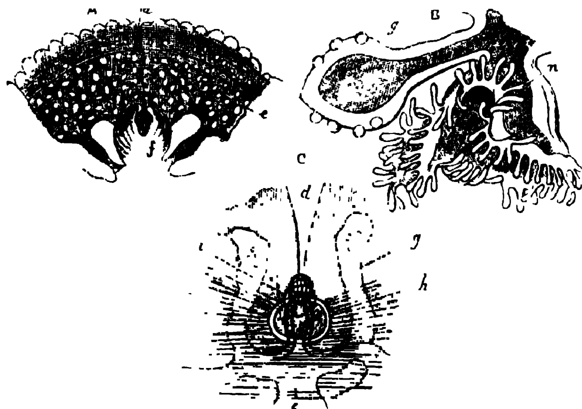


Fig. 20.—*Cephea ocellata* (?).—A, part of the umbrella, viewed from below, to show the plaited genital membrane (*f*) and the divided attachment of one of the pillars; *d*, place of one of the lithocysts. B, one of the oral pores (*m*) surrounded by tentacula (*n*); *g*, one of the clavate tentacles interspersed between the oral pores. C, one of the pedunculated lithocysts (*i*) in its notch (*d*) seen from below, with the oval plate from which muscular fibres (*h*) take their origin; *e*, the radiating canal with its cæcal lateral branches, *g*.

In most of the *Rhizostomidæ,* not only do the edges of the lips unite, but the opposite walls of the hydranth beneath the umbrella are, as it were, pushed in, so as to form four chambers, the walls of which unite, become perforated, and thus give rise to a sub-umbrellar cavity with a roof formed

* 'Mém. de l'Acad. de St. Pétersbourg,' xvi., 1870.

by the umbrella and a floor, the *brachiferous disk*, suspended

Fig. 21.

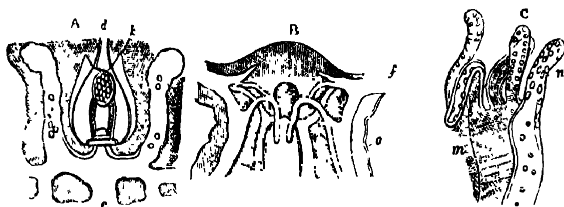


Fig. 21.—*Cephea ocellata* (?).—A, lithocyst enlarged with its hood (*k*) and the aboral pore of the canal (*e*) ; *d*, the notch of the margin of the umbrella. B, the brachiferous disk with the origins of the arms ; *f*, endoderm ; *o*, ectoderm. C, tentaculate lip of an oral pore enlarged ; *m*, oral cavity ; *n*, nematocysts.

by four pillars. In the roof the plaited genital membranes are developed. The floor (Fig. 21, B) gives off the subdivided

Fig. 22.

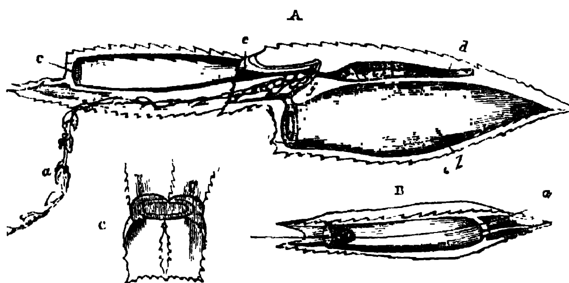


Fig. 22.—A, *Diphyes appendiculata.*—*a*, hydranths and hydrophyllia on the hydrosoma ; *b*, proximal nectocalyx ; *c*, aperture of distal nectocalyx ; *d*, somatocyst ; *e*, prolongation of the distal nectocalyx, by which it is attached to the hydrosoma ; *f*, point of attachment of the hydrosoma in the cavity, or hydrœcium, of the proximal nectocalyx. B, the distal nectocalyx with the canal (through which the bristle *a* is passed), which is traversed by the hydrosoma in A. C, extremity of the distal nectocalyx, with its muscular velum.

arms, the free margins of which bear the oral pores, and

which are traversed by canals which unite, pass through the pillars, and open into the central cavity of the umbrella.*

Fig. 23.

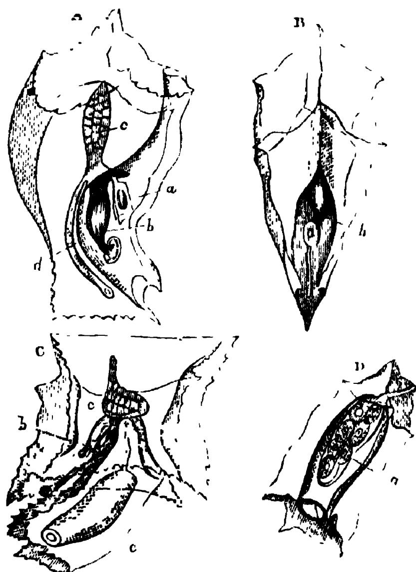


Fig. 23.—A, B, Diphyzooid (*Sphenoides*), lateral and front views. C, Diphyzooid of *Abyla* (*Cuboides*). *a*, *e*, gonophore or reproductive organ. *b*, hydranth; *c*, phyllocyst or cavity of hydrophyllium, with its process (*d*). D, free gonophore, its manubrium (*a*) containing ova.

* The species of *Cephea* the anatomy of which is here given, was obtained in the South Pacific near the Louisiade Archipelago, on the 11th of July, 1849. The aboral surface of the umbrella was of a brownish-grey colour, variegated with oval white spots: the oral surface, light brown with eight bluish-green lines radiating towards the lithocysts: the brachia grey with brown dots. The brachia divide into two at their origin, and then subdivide into an infinity of small branches. The general colour of the smaller branches is light brown, the small interspersed clavate tentacles being white. The long tentacles which terminate each brachium, are blue and cylindrical at their origin, but become

spherical nematocysts. In the sacculus, the cavity is wider. One wall is very thick, and multitudes of elongated nematocysts, the lateral series of which are sometimes larger than the rest, are disposed parallel with one another, and perpendicular to the surface of the sac. Like the other

Fig. 26.

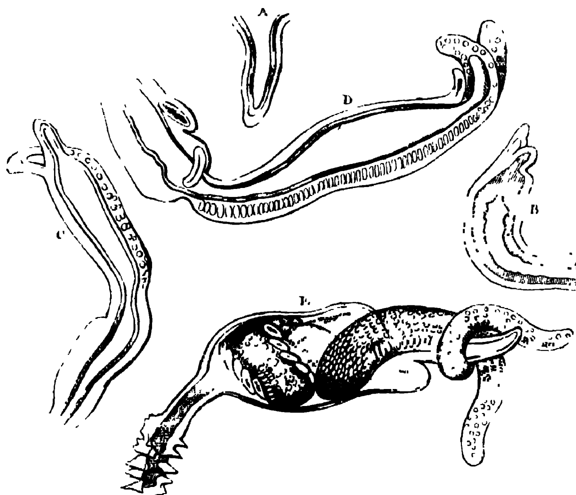


Fig. 26.—*Athorybia rosacea.*—The ends of the tentacular branches in various stages of development. A, lateral branch, commencing as a bud from the tentacle. In B, terminal papillæ, the rudiments of the filaments, are developed at the extremity of the branch; and, in C, the sacculus is beginning to be marked off, and thread cells have appeared in its walls; in D, the division into involucrum and sacculus is apparent; in E, the involucrum has invested the sacculus, the extremity of which is straight, while the lateral processes have curled round it.

organs, each of these tentacular appendages commences as a simple diverticulum of the ectoderm and endoderm, and passes through the stages represented in Fig. 26.

In *Physalia* the tentacula may be several feet long. They have no lateral branches, but the large nematocysts are

situated in transverse reniform thickenings of the wall of the tentacle, which occur at regular intervals.

Hydrophyllia are generally present, and, like the tentacula, are developed either from the pedicle of a hydranth, in which case they enclose the hydranth with its tentacle and a group of gonophores (*Calycophoridæ*), or, independently of the hydranths, from the cœnosarc (many *Physophoridæ*).

The hydrophyllia are transparent, and often present very beautifully defined forms, so that they resemble pieces of cut glass. They are composed chiefly of the ectoderm (and mesoderm) but contain a prolongation of the endoderm, with a corresponding diverticulum of the somatic cavity. They are, in fact, developed as cæcal processes of the endoderm and ectoderm; but the latter, with the mesodermal layer, rapidly predominates.

The gonophores of the *Siphonophora* present every variety, from a simple form, in which the medusoid remains in a state of incomplete development, to free medusoids of the Gymnophthalmatous type. As an example of the former condition the gonophores of *Athorybia* may be cited (Fig. 27); of the latter, the gonophores of *Physalia, Porpita,* and *Velella.*

In *Athorybia,* groups of gonophores, together with pyriform sacs, which resemble incompletely developed hydranths (*hydrocysts*) (Fig. 27, A, *a*), are borne upon a common stem, and constitute a *gonoblastidium* (Fig. 27, A). The groups of male and female gonophores (Fig. 27, A, *b, c*) are borne upon separate branches of the gonoblastidium (*androphores* and *gynophores*). Each female gonophore contains only a single ovum, which projects into the cavity of the imperfectly differentiated manubrium, and narrowing its cavity at different points gives rise to the irregular canals (Fig. 27, D, *d*). In the male gonophore, the nectocalyx is more distinct from the manubrium, and its extremity has a rounded aperture (Fig. 27, E).

In the *Calycophoridæ,* as in the elongated *Physophoridæ,* the development of new hydranths and their appendages, which is constantly occurring, takes place at that end of the

(Fig. 13, 4). It is sometimes small, relatively to the hydrosoma (*Agalma, Physophora*), sometimes so large (*Athorybia*, (Fig. 24), *Physalia, Porpita, Velella*), that the whole hydrosoma becomes the investment of the pyriform or discoidal air-sac; while the latter is sometimes converted into a sort of hard inner shell, its cavity being subdivided by septa into numerous chambers (*Porpita, Velella*).

Nectocalyces may be present or absent in the *Physophoridæ*. When present, their number varies, but they are confined to the region of the hydrosoma which lies nearest to the pneumatophore.

In the great majority of the *Hydrozoa*, the ovum undergoes cleavage and conversion into a morula, and subsequently into a planula, possessing a central cavity enclosed in a double cellular wall, the inner layer of which constitutes the hypoblast, and the outer the epiblast.

In most *Hydrophora* the ciliated, locomotive, planula becomes elongated and fixed by its aboral pole. At the opposite end, the mouth appears and the embryo passes into the gastrula stage. Tentacles next bud out round the mouth, and to this larval condition, common to all the *Hydrophora*, Allman has given the name of *Actinula*.

Generally, the embryo fixes itself by its aboral extremity at the end of the planula stage; but, in certain *Tubularidæ*, while the embryo is still free, a circlet of tentacles is developed close to the aboral end; and this form of larva differs but very slightly from that which is observed in the *Discophora*.

In the genus *Pelagia*, for example, the tentacles are developed from the circumference of the embryo, midway between the oral and aboral poles; but it neither fixes itself nor elongates into the ordinary actinula-form. On the contrary, it remains a free-swimming organism, and, by degrees, that moiety of the body which lies on the aboral side of the tentacular circlet widens and is converted into the umbrella, the other moiety becoming the hydranth, or "stomach," of the Medusa.

In *Lucernaria*, it is probable that the larva fixes itself before or during the development of the umbrella, and passes directly into the adult condition. But, in most *Discophora*, the embryo becomes a fixed actinula (the so-called *Hydra tuba* or *Scyphistoma*, Fig. 28, I.) multiplies agamogenetically by budding, and gives rise to permanent colonies of Hydriform polypes. At certain seasons of the year, some of these enlarge and undergo a further agamogenetic multiplication by fission (Fig. 28, II.). In fact, each divides transversely into a number of eight-lobed discoidal medusoids ("*Ephyræ*" or "*Medusæ bifidæ*," Fig. 28, II. and III.), and thus passes into what has been termed the *Strobila* stage. The *Ephyræ* becoming detached from one another and from the stalk of the *Strobila*, are set free, and, undergoing a great increase in size, take on the form of the adult Discophore, and acquire reproductive organs. The base of the *Strobila* may develope tentacles, (Fig. 28, II.) and resume the *Scyphistoma* condition.

Metschnikoff* has recently traced out the development of *Geryonia* (*Carmarina*), *Polyxenia*, *Æginopsis*, and other Discophora, which differ from the foregoing in possessing a velum; and in these, as in the *Trachynema ciliatum*, observed by Gegenbaur,† the process appears to be of essentially the same nature as in *Pelagia*. The *Scyphistoma* of *Aurelia*, *Cyanœa* and their allies is probably to be regarded, like the larva of *Pelagia*, as a Discophore with a rudimentary disk; in which case, the production of the *Ephyra*-forms of young *Discophora* will not be comparable to the development of medusoid gonophores among the *Hydrophora*, but will merely be a process of multiplication, by transverse fission, of a true, though undeveloped, Discophore.

In the *Siphonophora*,‡ the result of yelk division is the formation of a ciliated body consisting of a small-celled ectoderm investing a solid mass of large blastomeres, which

* "Studien über die Entwickelung der Medusen und Siphonophoren." ('Zeitschrift für Wiss. Zool.,' xxiv.)

† 'Zur Lehre der Generationswechsel,' 1854.

‡ See especially the late observations of Metschnikoff, *loc. cit.*

Fig. 28.

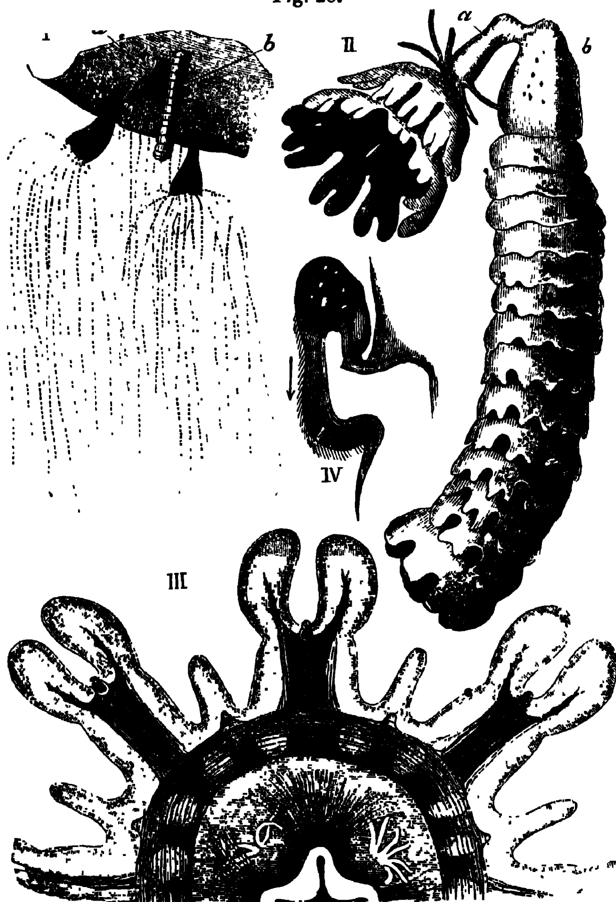


Fig. 28.—Figs. I. and II.—*Cyanæa capillata* (after Van Beneden.*)
I. Two *Hydræ tubæ* (*Scyphistoma* stage), exhibiting their ordinary characters, and between them two (*a*, *b*,) which are undergoing fission (*Strobila* stage).

* 'Recherches sur la Faune littorale de Belgique. Polypes.' 1866.

II. The two *Strobilæ*, *a* and *b*, three days later. In *a*, tentacles are developed, beneath the lowest of the *Ephyræ*, from the stalk of the *Strobila*, which will persist as a *Hydra tuba*.

III. Half the disk of an *Ephyra* of *Aurelia aurita*, seen from the oral face. The small tentacles which lie between the mouth and the band of circular muscular fibres are inside the somatic cavity, whence sixteen short and wide radial canals extend to the periphery, where they are united by transverse branches. Eight of the radial canals enter the corresponding lobes, and finally divide into three branches; one which enters the peduncle of the lithocyst, and two lateral cæca. Radiating bands of muscular fibres accompany these canals.

IV. Side view of one of the lithocysts with its peduncle. The arrow indicates the direction in which the cilia of the exterior work.

eventually pass into the cells of the endoderm. This body does not take the form of an actinula. On the contrary, it appears to be the rule that buds from which a hydrophyllium, a nectocalyx, a tentacle, or pneumatophore, or even all of them, will be developed, take their origin antecedently to the formation of the first polypite and of the gastric cavity.

As Metschnikoff well remarks, the mode of development of the *Siphonophora* is wholly inconsistent with the doctrine that the various appendages of the hydrosoma in these animals represent individuals. The *Hydrozoa* are not properly compound organisms, if this phrase implies a coalescence of separate individualities; but they are organisms, the organs of which tend more or less completely to become independent existences, or zooids. A medusoid, though it feeds and maintains itself, is, in a morphological sense, simply the detached independent generative organ of the hydrosoma on which it was developed; and what is termed the "alternation of generations," in these and like cases, is the result of the dissociation of those parts of the organism on which the generative function devolves, from the rest.*

In certain *Discophora* belonging to the group of *Trachynemata*, a method of multiplication by gemmation has been

* I have seen no reason to depart from the opinions on the subject of "Animal individuality" enunciated in my lecture published in the 'Annals and Magazine of Natural History' for June 1852.

observed, which is unknown among the other *Hydrozoa*. It may be termed *entogastric* gemmation, the bud growing out from the wall of the gastric cavity, into which it eventually passes on its way outwards; while, in all other cases, gemmation takes place by the formation of a diverticulum of the whole wall of the gastro-vascular cavity, which projects on to the free surface of the body, and is detached thence (if it become detached), at once, into the circumjacent water. The details of this process of entogastric gemmation have been traced by Haeckel* in *Carmarina hastata*, one of the *Geryonidæ*. As in other members of that family, a conical process of the mesoderm, covered by the endoderm, projects from the roof of the gastric cavity and hangs freely down into its interior. Upon the surface of this, minute elevations of $\frac{1}{500}$th of an inch in diameter make their appearance. The cells of which these outgrowths are composed next become differentiated into two layers—an external clear and transparent layer, which is in contact with the cone, and invests the sides of the elevation; and an inner darker mass. The external layer is the ectoderm of the young medusoid, the inner its endoderm. A cavity, which is the commencement of the gastric cavity, appears in the endodermal mass, and opens outwards on the free side of the bud. The latter, now $\frac{1}{250}$th of an inch in diameter, has assumed the form of a plano-convex disk, fixed by its flat side to the cone, and having the oral aperture in the centre of its convex free side. The disk next increasing in height, the body acquires the form of a flask with a wide neck. The belly of the flask is the commencement of the umbrella of the budding medusoid; the neck is its gastric division. The belly of the flask, in fact, continues to widen out until it has the form of a flat cup, from the centre of which the relatively small gastric neck projects, and the bud is converted into an unmistakable medusoid, attached to the cone by the centre of the aboral face of its umbrella. In the meanwhile, the gelatinous transparent mesoderm has appeared, and, in the umbrella, has acquired a great rela-

* 'Beiträge zur Naturgeschichte der Hydromedusen,' 1865.

tive thickness. Into this, eight prolongations of the gastric cavity extend, and give rise to the radial canals, which become united into a circular canal at the circumference of the disk. The velum, tentacula, and lithocysts are developed, and the bud becomes detached as a free swimming medusoid. But this medusoid is very different from the *Carmarina* from which it has budded. For example, it has eight radial canals, while the *Carmarina* has only six; it has solid tentacles, while the adult *Carmarina* has tubular tentacles; it has no gastric cone, and has differently disposed lithocysts. Haeckel, in fact, identifies it with *Cunina rhododactyla*, a form which had hitherto been considered to be not only specifically and generically different from *Carmarina*, but to be a member of a distinct family—that of the *Æginidæ.*

What makes this process of asexual multiplication more remarkable is, that it takes place in *Carmarinæ* which have already attained sexual maturity, and in males as well as in females.

There is reason to believe that a similar process of entogastric proliferation occurs in several other species of *Æginidæ.*—*Ægineta prolifera* (Gegenbaur), *Eurystoma rubiginosum* (Kölliker), and *Cunina Köllikeri* (F. Muller); but, in all these cases, the medusoids which result from the gemmative process closely resemble the stock from which they are produced.

As might be expected, the *Hydrozoa* are extremely rare in the fossil state, and probably the last animal the discovery of fossil remains of which could be anticipated, is a jelly-fish. Nevertheless, some impressions of Medusæ, in the Solenhofen slates, are sufficiently well preserved to allow of their determination as members of the group of *Rhizostomidæ.** The apparent absence of the remains of *Hydrophora* in the mesozoic and newer palæozoic rocks, is very remarkable. Some singular organisms, termed *Grap-*

* Haeckel, "Ueber zwei neue fossile Medusen aus der Familie der Rhizostomiden." ('Jahrbuch für Mineralogie,' 1866.)

tolites, which abound in the Silurian rocks, may possibly be *Hydrozoa*, though they present points of resemblance with the *Polyzoa*. They are simple or branched stems, sometimes slender, sometimes expanded or foliaceous; occasionally the branches are connected at their origin by a membranous expansion. The stems are tubular, and beset on one or both sides with minute cup-shaped prolongations, like the thecæ of a Sertularian. A solid thickening of the skeleton may have the appearance of an independent axis. Allman has suggested that the theciform projections of the Graptolite stem may correspond with the nematophores of Sertularians, and that the branches may have been terminated by hydranths. Appendages which appear to be analogous to the gonophores of the *Hydrophora*, have been described in some Graptolites.*

With a very few exceptions (*Hydra*, *Cordylophora*,) the *Hydrozoa* are marine animals; and a considerable number, like the *Calycophoridæ* and *Physophoridæ*, are entirely pelagic in their habits.

The Actinozoa.—The essential distinctions between the *Actinozoa* and the *Hydrozoa* are two. In the first place, the oral aperture of an Actinozoon leads into a sac, which, without prejudice to the question of its exact function, may be termed "gastric," and which is not, like the hydranth of the Hydrozoon, free and projecting, but is sunk within the body. From the walls of the latter, it is separated by a cavity, the sides of which are divided by partitions, the *mesenteries*, which radiate from the wall of the gastric sac to that of the body, and divide the somatic cavity into a corresponding number of *intermesenteric chambers*. As the gastric sac is open at its inner end, however, its cavity is in free communication with that of the central space which communicates with the intermesenteric chambers; and the central space, together with the chambers, which

* Hall: 'Graptolites of the Quebec Series of North America,' 1865. Nicholson: 'Monograph of the British Graptolitidæ,' 1872.

are often collectively termed the "body cavity" or "perivisceral cavity," are, in reality, one with the digestive cavity, and, as in the *Hydrozoa*, constitute an *enterocœle*. Thus an Actinozoon might be compared to a *Lucernaria*, or still better to a *Carduella*, in which the outer face of the hydranth is united with the inner face of the umbrella; under these circumstances the canals of the umbrella in the Hydrozoon would answer to the intermesenteric chambers in the Actinozoon.

Secondly, in the *Actinozoa*, the reproductive elements are developed in the walls of the chambers or canals of the enterocœle, just as they so commonly are in the walls of the gastro-vascular canals of the *Hydrozoa*, but the generative organs thus constituted do not project outwardly, nor discharge their contents directly outwards. On the contrary, the ova and spermatozoa are shed into the enterocœle, and eventually make their way out by the mouth. In this respect, again, the Actinozoon is comparable to a *Lucernaria* modified by the union of the hydranth with the ventral face of the umbrella; under which circumstances the reproductive elements, which, in all *Hydrozoa*, are developed, either in the walls of the hydranth or in those of the oral face of the umbrella, would be precluded from making their exit by any other route than through the gastro-vascular canals and the mouth.

In the fundamental composition of the body of an ectoderm and endoderm, with a more or less largely developed mesoderm, and in the abundance of thread-cells, the *Actinozoa* agree with the *Hydrozoa*.

In most of the *Actinozoa*, the single polype, into which the embryo is converted, gives rise by budding to many zooids which form a coherent whole, termed by Lacaze-Duthiers, a *zoanthodeme*.

The Coralligena.—The *Actinozoa* comprehend two groups—the *Coralligena* and the *Ctenophora*,—which are widely different in appearance, though fundamentally similar in structure. In the former, the mouth is always surrounded by one or more circlets of tentacles, which may be slender

and conical, or short, broad and fimbriated. The mouth is usually elongated in one direction, and, at the extremities of the long diameter, presents folds which are continued into the gastric cavity. The arrangement of the parts of the body is therefore not so completely radiate as it appears to be. The enterocœle is divided into six, eight, or more, wide intermesenteric chambers, which communicate with the cavities of the tentacles, and sometimes, directly with the exterior, by apertures in the parietes of the body. The mesenteries which separate these wide chambers are thin

Fig. 29.

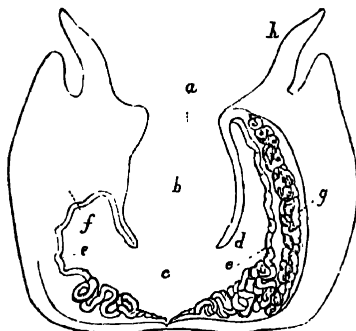


Fig. 29.—Perpendicular section of *Actinia holsatica* (after Frey and Leuckart).—*a*, mouth; *b*, gastric cavity; *c*, common cavity, into which the gastric cavity and the intermesenteric chambers open; *d*, intermesenteric chambers; *e*, thickened free margin, containing thread-cells of, *f*, a mesentery; *g*, reproductive organ; *h*, tentacle.

and membranous. Two of them, at opposite ends of a transverse diameter of the Actinozoon, are often different from the rest. Each mesentery ends, at its aboral extremity, in a free edge, often provided with a thickened and folded margin; and these free edges look towards the centre of an axial cavity,* into which the gastric sac and all the intermesenteric chambers open.

In the *Coralligena*, the outer wall of the body is not pro-

* Partially digested substances are often found in this axial space, and it is not improbable that it may functionally represent the stomach or the commencement of the intestine in higher animals.

vided with bands of large paddle-like cilia. Most of them are fixed temporarily or permanently, and many give rise by gemmation to turf-like, or arborescent, zöanthodemes. The great majority possess a hard skeleton, composed principally of carbonate of lime, which may be deposited in permanently disconnected spicula in the walls of the body; or the spicula may run into one another, and form solid networks, or dense plates, of calcareous matter. When the latter is the case, the calcareous deposit may invade the base and lateral walls of the body of the Actinozoon, thus giving rise to a simple cup, or *theca*. The skeleton thus formed, freed of its soft parts, is a "cup-coral," and receives the name of a *corallite*.

In a zoanthodeme, the various polypes (*anthozooids*), formed by gemmation may be distinct, or their several enterocœles may communicate; in which last case, the common connecting mass of the body, or *cœnosarc*, may be traversed by a regular system of canals. And, when such compound *Actinozoa* develope skeletons, the corallites may be distinct, and connected only by a substance formed by the calcification of the cœnosarc, which is termed *cœnenchyma;* or the thecæ may be imperfectly developed, and the septa of adjacent corallites run into one another. There are cases, again, in which the calcareous deposit in the several polypes of a compound Actinozoon, and in the superficial parts of the cœnenchyma, remains loose and spicular, while the axial portion of the cœnosarc is converted into a dense chitinous or calcified mass—the so-called *sclerobase*.

The mesoderm contains abundantly developed muscular fibres. The question whether the *Coralligena* possess a nervous system and organs of sense, hardly admits of a definite answer at present. It is only in the *Actinidæ* that the existence of such organs has been asserted; and the nervous circlet of *Actinia*, described by Spix, has been seen by no later investigator, and may be safely assumed to be non-existent. Professor P. M. Duncan, F.R.S.,* how-

* 'On the Nervous System of Actinia.' (Proceedings of the Royal Society, October 9, 1873.)

ever, has recently described a nervous apparatus, consisting of fusiform ganglionic cells, united by nerve fibres, which resemble the sympathetic nerve fibrils of the *Vertebrata*, and form a plexus, which appears to extend throughout the pedal disk, and very probably into other parts of the body. In some of the *Actinidæ* (*e.g.*, *Actinia mesembryanthemum*), brightly coloured bead-like bodies are situated in the oral disk outside the tentacles. The structure of these "chromatophores," or "bourses calicinales," has been carefully investigated by Schneider and Rötteken, and by Professor Duncan. They are diverticula of the body wall, the surface of which is composed of close-set "bacilli," beneath which lies a layer of strongly-refracting spherules, followed by another layer of no less strongly-refracting cones. Subjacent to these, Professor Duncan finds ganglion cells and nerve plexuses. It would seem, therefore, that these bodies are rudimentary eyes.

The sexes are united or distinct, and the ovum is ordinarily, if not always, provided with a vitelline membrane. The impregnated ovum gives rise to a ciliated morula, which may either be discharged or undergo further development within the somatic cavity of the parent. The morula becomes a gastrula, but whether by true invagination or by delamination, as in most of the *Hydrozoa*, is not quite clear. The gastrula usually fixes itself by its closed end, while tentacles are developed from its oral end. It can hardly be doubted that the intermesenteric chambers are diverticula of the primitive enterocœle; but the exact mode of their origin needs further elucidation.

Lacaze-Duthiers * has recently thrown a new light upon the development of the *Coralligena*, and particularly of the *Actiniæ* (*Actinia*, *Sagartia*, *Bunodes*). These animals are generally hermaphrodite, testes and ovaria being usually found in the same animal, and even in the same mesenteries; but it may happen that the organs of one or the other sex are, at any given time, exclusively developed. The ova

* "Développement des Coralliaires." ('Archives de Zoologie expérimentale,' 1872.)

undergo the early stages of their development within the body of the parent. The process of yelk division was not observed, and in the earliest condition described the embryo was an oval planula-like body, composed of an inner coloured substance and an outer colourless layer. The outer layer (epiblast = ectoderm) soon becomes ciliated. An oval depression appears at one end, and becomes the mouth * and gastric sac, while, at the opposite extremity, the cilia elongate into a tuft. The ectoderm extends into and lines the gastric sac, while the interior of the coloured hypoblast becomes excavated by a cavity, the enterocœle, which communicates with the gastric sac. In this condition the embryo swims about with its oral pole directed backwards.

The oral aperture changes its form and becomes elongated in one direction, which may be termed the oral axis. The mesenteries are paired processes of the transparent outer layer (probably of that part which constitutes the mesoderm) which mark off corresponding segments of the enterocœle. The first which make their appearance are directed nearly at right angles to the oral axis near, but not exactly in, the centre of its length. Hence they divide the enterocœle into two primitive chambers, a smaller (A) at one end of the oral axis, and a larger (A′) at the other. This condition may be represented by A ∸ A′; the dots indicating the position of the primitive mesenteries, and the hyphen that of the oral axis. It is interesting to remark that, in this state, the embryo is a bilaterally symmetrical cylindrical body, with a central canal, the future gastric sac; and, communicating therewith, a bilobed enterocœle, which separates the central canal from the body wall. In fact, in principle, it resembles the early

* Kowalewsky describes the formation of a gastrula by invagination in a species of *Actinia* and in *Cereanthus*, the aperture of invagination becoming the mouth (Hofmann and Schwalbe, 'Jahresbericht,' Bd. II. p. 269). In other species of *Actinia* and in *Alcyonium*, the planula seems to delaminate. Ordinary yelk division occurs in some *Anthozoa*, while in others (*Alcyonium*) the process rather resembles that which occurs in most Arthropods.

condition of the embryo of a Ctenophore, a Brachiopod, or a *Sagitta*.

Another pair of mesenteric processes now makes its appearance in the larger chamber A′, and cuts off two lateral chambers, BB, which lie between these secondary mesenteries and the primary ones. In this state the enterocœle or somatic cavity is four-chambered $\left(A \ \div\frac{B}{B}\ A'\right)$. Next a third pair of mesenteries appear in the smaller chamber (A), and divide it into three portions, one at the end of the oral axis (A), and two lateral (CC). In this stage there are therefore six chambers $\left(A\ \frac{C}{C}\div\frac{B}{B}\ A'\right)$; but almost immediately the number is increased to eight, by the development of a fourth pair of mesenteries in the chambers B, B, which thus give rise to the chambers D, D, between the primitive mesenteries and themselves. The embryo remains in the eight-chambered condition $\left(A\ \frac{C'}{C'}\div\frac{D\ B}{D\ B}\ A'\right)$ for some time, until all the chambers and their dividing mesenteries become equal. Then a fifth and a sixth pair of mesenteries are formed in the chambers C, C, and D, D; two pairs of new chambers, E and F, are produced, and thus the *Actinia* acquires twelve chambers $\left(A\ \frac{C\ E}{C\ E}\div\frac{F\ D\ B}{F\ D\ B}\ A'\right)$, five of which result from the subdivision of the smaller primary chamber, and seven from that of the larger primary chamber. The various chambers now acquire equal dimensions, and the tentacles begin to bud out from each. The appearance of the tentacles, however, is not simultaneous. That which proceeds from the chamber A′ is earliest to appear, and for some time is largest, and, at first, eight of the tentacles are larger than the other four.

The coiled marginal ends of the mesenteries appear at first upon the edges of the two primary mesenteries; then upon the edge of the fourth pair, and afterwards upon those of the other pairs.

For the further changes of the young *Actinia*, I must refer to the work cited. Sufficient has been said to show that the development of the *Actiniæ* follows a law of bilateral symmetry, and to bring out the important fact that, in the course of its development, the finally hexamerous Anthozoon passes through a tetramerous and an octomerous stage.

Phenomena analogous to the "alternation of generations," which is so common among the *Hydrozoa*, are unknown among the great majority of the *Actinozoa*. But Semper * has recently described a process of agamogenesis in two species of *Fungiæ*, which he ranks under this head. The *Fungiæ* bud out from a branched stem, and then become detached and free, as is the habit of the genus. To make the parallel with the production of a medusoid from a hydroid polype complete, however, the stem should be nourished by a sexless anthozooid of a different character from the forms of *Fungiæ* which are produced by gemmation. And this does not appear to be the case.

In one division of the *Coralligena*—the *Octocoralla*—eight enterocœle chambers are developed, and as many tentacles. Moreover, these tentacles are relatively broad, flattened, and serrated at the edges, or even pinnatifid. The Actinozoon developed from the egg may remain simple (*Haimea*, Milne-Edwards), but usually gives rise to a zoanthodeme.

The cœnosarc of the zoanthodeme in the *Octocoralla* is a substance of fleshy consistence, which is formed chiefly of a peculiar kind of connective tissue, containing many muscular fibres developed in the thickened mesoderm. The axial cavity of each anthozooid is in communication with a system of large canals. In *Alcyonium*, a single large canal descends from each anthozooid into the interior of the zoanthodeme, and the eight mesenteries are continued as so many ridges throughout its entire length,† so that these tubes have been compared to the thecal canals of the Mille-

* 'Ueber Generations-Wechsel bei Steinkorallen.' Leipzig, 1872.

† Pouchet and Myèvre, "Contribution à l'Anatomie des Alcyonaires." ('Journal d'Anatomie et de la Physiologie,' 1870.)

Fig. 30.

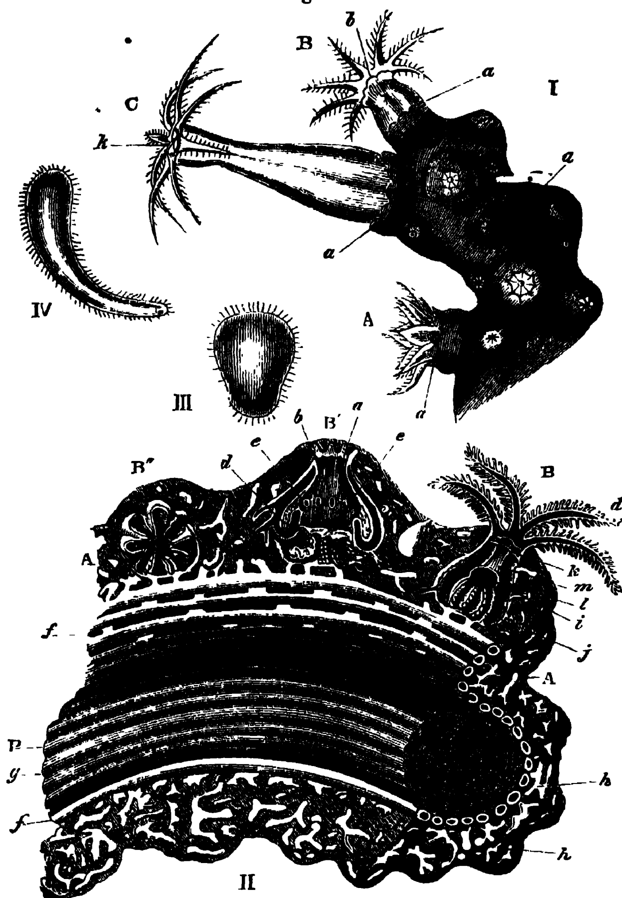


Fig. 30.—*Corallium rubrum* (after Lacaze-Duthiers *).
1. The end of a branch with A, B, C, three anthozooids in different degrees of expansion; *k*, the mouth; *a*, that part of the cœnosarc which rises into a cup around the base of each anthozooid.

* 'Histoire Naturelle du Corail,' 1864.

II. Portion of a branch, the cœnosarc of which has been divided longitudinally and partially removed; B, B′, B″, anthozooids in section; B, anthozooid with expanded tentacles; *k*, mouth; *m*, gastric sac; *i*, its inferior edge; *j*, mesenteries.
B′, anthozooid retracted, with the tentacles (*d*) drawn back into the intermesenteric chambers; *c*, orifices of the cavities of the invaginated tentacles; *e*, circum-oral cavity; *b*, the part of the body which forms the projecting tube when the anthozooid is expanded; *a*, festooned edges of the cup.
B″, anthozooid, showing the transverse sections of the mesenteries.
A, A, Cœnosarc, with its deep longitudinal canals (*f*), and superficial, irregular, reticulated canals (*h*). P, The hard axis of the coral, with longitudinal grooves (*g*) answering to the longitudinal vessels.
III., IV. Free ciliated embryos.

pores. In the red coral of commerce (*Corallium rubrum*, Fig. 30), the large canals run parallel with the axial skeleton. A delicate network, which traverses the rest of the substance of the cœnosarc, appears to be sometimes solid and sometimes to form a system of fine canals opening into the larger ones. The anthozooids possess numerous muscles by which their movements are effected. The fibres are delicate, pale, and not striated. Nerves have not been certainly made out.

It is in these *Octocoralla* that the form of skeleton which is termed a *sclerobase*, which is formed by cornification or calcification of the axial connective tissue of the zoanthodeme, occurs. It is an unattached simple rod in *Pennatula* and *Veretillum*, but fixed, tree-like, branched, and even reticulated, in the *Gorgoniæ* and the red coral of commerce (*Corallium*). In the *Alcyonia*, or "Dead men's fingers," of our own shores, there is no sclerobase, nor is there any in *Tubipora*, the organ coral. But, whereas in all the other *Octocoralla* the bodies of the polypes and the cœnosarc are beset with loose spicula of carbonate of lime, *Tubipora* is provided with solid tubiform thecæ, in which, however, there are no septa.

Dimorphism has been observed by Kölliker to occur extensively among the *Pennatulidæ*. Each zoanthodeme presents at least two different sets of zooids, some being fully developed, and provided with sexual organs, while the others have neither tentacles nor generative organs, and

exhibit some other peculiarities.* These abortive zooids are either scattered irregularly among the others (*e.g.* *Sarcophyton*, *Veretillum*), or may occupy a definite position (*e.g.* *Virgularia*).

In the other chief division of the *Coralligena*—the *Hexacoralla*—the fundamental number of enterocœle chambers and of tentacles is six,† and the tentacles are, as a rule, rounded and conical, or filiform.

The Actinozoon developed from the egg in some of the *Hexacoralla* remains simple, and attains a considerable size. Of these—the *Actinidæ*—many are to some extent locomotive, and some (*Minyas*) float freely by the help of their contractile pedal region. The most remarkable form of this group is the genus *Cereanthus*, which has two circlets, each composed of numerous tentacles, one immediately around the oral aperture, the other at the margin of the disk. The foot is elongated, subconical, and generally presents a pore at its apex. Of the diametral folds of the oral aperture, one pair is much longer than the other, and is produced as far as the pedal pore. The larva is curiously like a young hydrozoon with four tentacles, and, at one time, possesses four mesenteries.

The *Zoanthidæ* differ from the *Actinidæ* in little more than their multiplication by buds, which remain adherent, either by a common connecting expansion or by stolons; and in the possession of a rudimentary, spicular, skeleton. In the *Antipathidæ* there is a sclerobasic skeleton. The proper stone-corals are essentially *Actiniæ*, which become converted into zoanthodemes by gemmation or fission, and develope a continuous skeleton.

The skeletal parts ‡ of all the *Actinozoa*, consist either of a substance of a horny character; or of an organic basis impregnated with earthy salts (chiefly of lime and magnesia), but which can be isolated by the action of dilute

* 'Abhandlungen der Senkenbergischen Naturforschenden Gesellschaft,' Bd. vii. viii.

† That is to say, in the adult, they are either six or some multiple of six.

‡ See Kölliker, 'Icones Histologicæ,' 1866.

acids; or finally, of calcareous salts in an almost crystalline state, forming rods or corpuscles, which, when treated with acids, leave only an inappreciable and structureless film of organic matter. The hard parts of all the *Aporosa*, *Perforata*, and *Tabulata* of Milne-Edwards are in the last-mentioned condition; while, in the *Octocoralla*, except *Tubipora*, and in the *Antipathidæ*, and *Zoanthidæ*, among the *Hexacoralla*, the skeleton is either horny; or consists, at any rate, to begin with, of definitely formed spicula, which contain an organic basis, and frequently present a laminated structure. In the organ coral (*Tubipora*), the skeleton has the character of that of the ordinary stone-corals, except that it is perforated by numerous minute canals.

The skeleton appears, in all cases, to be deposited within the mesoderm, and in the intercellular substance of that layer of the body. Even the definitely shaped spicula of the *Octocoralla* seem not to result from the metamorphosis of cells. In the simple aporose corals the calcification of the base and side walls of the body, gives rise to the cup or *theca*; from the base the calcification extends upwards in lamellæ, which correspond with the interspaces between the mesenteries, and gives rise to as many vertical *septa*,* the spaces between which are termed *loculi*; while, in the centre, either by union of the septa or independently, a column, the *columella*, grows up. Small separate pillars between the columella and the septa are termed *paluli*. From the sides of adjacent septa scattered processes of calcified substance, or *synapticulæ*, may grow out toward one another, as in the *Fungidæ*; or the interruption of the cavities of the loculi may be more complete in consequence of the formation of shelves stretching from septum to septum, but lying at different heights in adjacent loculi. These are *interseptal dissepiments*. Finally, in the *Tabulata*, horizontal plates, which stretch completely across the cavity of the theca, are formed one above the other and constitute *tabular dissepiments*.

* Lacaze-Duthiers' investigations on *Astræa calycularis* prove that the septa begin to be formed before the theca.

In the *Aporosa* the theca and septa are almost invariably imperforate; but, in the *Perforata*, they present apertures, and, in some Madrepores, the whole skeleton is reduced to a mere network of dense calcareous substance. When the *Hexacoralla* multiply by gemmation or fission, and thus give rise to compound massive or arborescent aggregations, each newly-formed coral polype developes a skeleton of its own, which is either confluent with that of the others, or is united with them by calcification of the connecting substance of the common body. This intermediate skeletal layer is then termed *cœnenchyma.*

The septa in the adult *Hexacoralla* are often very numerous and of different lengths, some approaching the centre more closely than others do. Those of the same lengths are members of one 'cycle;' and the cycles are numbered according to the lengths of the septa, the longest being counted as the first. In the young, six equal septa constitute the first cycle. As the coral grows, another cycle of six septa arises by the development of a new septum between each pair of the first cycle; and then a third cycle of twelve septa divides the previously existing twelve interseptal chambers into twenty-four. If we mark the septa of the first cycle A, those of the second B, and those of the third C, then the space between any two septa (AA) of the first cycle will be thus represented when the third cycle is formed—A C B C A.

When additional septa are developed, the fourth and following cycles do not consist of more than twelve septa each; hence the septa of each new cycle appear in twelve of the previously existing interseptal spaces, and not in all of them; and the order of their appearance follows a definite law, which has been worked out by Milne-Edwards and Haime. Thus, the septa of the fourth cycle of twelve (d) bisect the interseptal space A C; and those of the fifth cycle (e) the interseptal space B C; the septa of the sixth cycle (f), A d and d A; those of the seventh cycle (g), e B and B e; those of the eighth cycle (h), d C and C d; and those of the ninth cycle (i), C e and e C.

Hence, after the formation of nine cycles, the septa added between every pair of primary septa (A, A) will be thus arranged—A f d h C i e g B g e i C h d f A.*

The stone-corals ordinarily known as *Millepores* are characterised by being traversed by numerous tubular cavities, which open at the surface, and the deeper parts of which are divided by numerous close-set transverse partitions, or *tabular dissepiments*, while vertical septa are rudimentary or altogether absent. These were regarded as *Anthozoa*, and classed together in the division of *Tabulata*, until the elder Agassiz † published his observations on the living *Millepora alcicornis*, which led him to the conclusion that the *Tabulata* are *Hydrozoa* allied to *Hydractinia*, and that the extinct *Rugosa* were probably of the same nature.

The evidence adduced by Agassiz, however, was insufficient to prove his conclusions; and the subsequent discovery by Verrill that another tabulate coral, *Pocillopora*, is a true Hexacorallan, while Moseley ‡ has proved that *Heliopora cœrulea* is an Octocorallan, gave further justification to those who hesitated to accept Agassiz' views.

The recent very thorough and careful investigation of a species of *Millepora* occurring at Tahiti,§ by Mr. Moseley, although it still leaves us in ignorance of one important point, namely, the characters of the reproductive organs, yet permits no doubt that *Millepora* is a true Hydrozoon allied to *Hydractinia*, as Agassiz maintained. The surface of the living *Millepora* presents short, broad hydranths, the mouth of which is surrounded by four short tentacles. Around each of these alimentary zooids is disposed a zone of from five to twenty or more, much longer, mouthless zooids, over the bodies of which numerous short tentacles are scattered. Each of these zooids expands at its base

* That the order of occurrence of the septa of various lengths, at the different stages of growth of a corallite, is that indicated, seems to be clear, whatever may be the exact mode of development of the septa in each cycle.

† 'Natural History of the United States,' vols. iii. and iv., 1860–62.

‡ Moseley, "The Structure and Relations of the Alcyonarian, *Heliopora cœrulea*," &c. (Proc. Royal Society, Nov. 1875.)

§ Proceedings of the Royal Society, 1876.

into a dilatation, whence tubular processes proceed, which ramify and anastomose, giving rise to a thin expanded hydrosoma. The calcareous matter (composed as usual of carbonate, with a small proportion of phosphate, of lime) forms a dense continuous crust upon the ectoderm of the ramifications of the hydrosoma, that part of it which underlies the dilatations of the zooids constituting the septa. As the first formed hydrosomal expansion is completed, another is formed on its outer surface, and it dies. The "thecal" canals of the coral arise from the correspondence in position of the dilatations of the zooids of successive hydrosomal layers, and the tabulæ are their supporting plates.

Thus the group of the *Tabulata* ceases to exist, and its members must be grouped either with the *Hexacoralla*, the *Octocoralla*, or the *Hydrozoa*.

The *Rugosa* constitute a group of extinct and mainly Palæozoic stone-corals, the thecæ of which are provided with tabular dissepiments, and generally have the septa less developed than those of the ordinary stone-corals. The arrangement of the parts of the adult *Rugosa* in fours, and the bilateral symmetry which they sometimes exhibit, are interesting peculiarities when taken in connection with the tetramerous and asymmetrical states of the embryonic *Hexacoralla*. On the other hand, some of the *Rugosa* possess opercula, which are comparable to the skeletal appendages of the Alcyonarian *Primnoa* observed by Lindström, and the tetramerous arrangement of their parts suggests affinity with the *Octocoralla*. It seems not improbable that these ancient corals represent an intercalary type between the *Hexacoralla* and the *Octocoralla*.

All the *Actinozoa* are marine animals. The *Actiniæ*, among the *Hexacoralla*, and various forms of *Octocoralla*, have an exceedingly wide distribution, while the latter are found at very great depths.

The stone-corals, again, have a wide range, both as respects depth and temperature, but they are most abundant

in hot seas, and many are confined to such regions. Some of these stone-corals are solitary in habit, while others are social, growing together in great fields, and forming what are called "coral reefs." The latter are restricted within that comparatively narrow zone of the earth's surface which lies between the isotherms of 60°, or, in other words, they do not extend for more than about 30° on either side of the equator. It is not conditions of temperature alone, however, which limit their distribution; for, within this zone, the reef-builders are not found alive at a greater depth than from fifteen to twenty fathoms, while, at the equator, an average temperature of 68° is not reached within a depth of 100 fathoms.

Not only heat, then, but light, and probably rapid and effectual aeration, are essential conditions for the activity of the reef-building *Actinozoa*. But, even within the coral zone, the distribution of the reef-builders appears to be singularly capricious. None are found on the west coast of Africa, very few on the east coast of South America, none on the west coast of North America; while in the Indian Ocean, the Pacific, and the Caribbean Sea, they cover thousands of square miles. It is by no means certain, however, that any one species of West India reef coral is identical with any East Indian species, and the corals of the central Pacific differ very considerably from those of the Indian Ocean.

Different species of Corals exhibit great differences as to the rapidity of their growth, and the depth at which they flourish best; and no one must be taken as evidence for another in these respects. Certain species of *Perforata* (*Madreporidæ* and *Poritidæ*) appear to be at once the fastest growers, and those which delight in the shallowest waters. The *Astræidæ* among the *Aporosa*, and *Seriatopora* among the *Tabulata*, live at greater depths, and are probably slower of increase.

Under the peculiar conditions of existence which have just been described, it would seem easy enough to comprehend, *à priori*, the necessary arrangement of coral reefs.

As the reef-building *Actinozoa* cannot live at greater depths than twenty fathoms, or thereabouts, it is clear that no reef can be originally formed at a greater depth below the surface, and such a depth usually implies no very great distance from land. Furthermore, we should expect that the growth of the coral would fill up all the space between the shore and this furthest limit of its growth; so that the shores of coral seas would be fringed by a sort of flat terrace of coral, covered, at most, by a very few feet of water; that this terrace would extend out until the shelving land upon which it had grown descended to a depth of some twenty fathoms; and that then it would suddenly end in a steep wall, the summit and upper parts of which would be crowned with overhanging ledges of living coral, while its base would be hidden by a talus of dead fragments, torn off and accumulated by the waves. Such a "fringing reef" as this, in fact, surrounds the island of Mauritius. The beach here does not gradually shelve down into the depths of the sea, but passes into a flat, irregular bank, covered by a few feet of water, and terminating at a greater or less distance from the shore in a ridge, over which the sea constantly breaks, and the seaward face of which slopes at once sheer down into fifteen or twenty fathoms of water.

The structure of a fringing reef varies at different distances from the land, and at different depths in its seaward face. The edge beaten by the surf is composed of living masses of *Porites*, and of the coral-like plant, the *Nullipore*; deeper than this is a zone of *Aporosa* (*Astræidæ*), and of Millepores (*Seriatopora*); while, deeper still, all living coral ceases; the lead bringing up either dead branches, or showing the existence of a flat gently sloping floor, the true sea-bottom, covered with fine coral-sand and mud. Passing from the edge of the reef landwards, the *Poritidæ* cease, and are replaced by a ridge of agglomerated dead branches and sand, coated with *Nullipore*; the floor of the shallow basin, or "lagoon," enclosed between the reef and the land, is formed by a conglomerate, composed of frag-

ments of coral cemented by mud; and, on this, *Meandrinæ* and *Fungiæ* rest and flourish, exhibiting the most gaudy coloration, and sometimes attaining a great size. During storms, masses of coral are hurled on to the floor of the lagoon, and there gradually increase the accumulation of rocky conglomerate; but in no other way can a fringing reef, which has once attained its limit in depth, increase in size, unless, indeed, the talus accumulating at the foot of its outer wall should ever rise sufficiently high to afford a footing for the corals within their prescribed limits of depth.

Such is the structure of a fringing reef; but the great majority of reefs in the Pacific are very different in their character. Along the north-eastern coasts of New Holland, for instance, a vast aggregation of reefs lies at a distance from the shore which varies from a hundred to ten miles; forming a mighty wall or barrier against the waves of the Pacific. At a few hundred yards outside this "barrier reef" no bottom can be obtained with a sounding line of a thousand fathoms; between the reef and the main land, on the contrary, the sea is hardly ever more than thirty fathoms deep. Many of the islands of the Pacific, again, are encircled with reefs corresponding exactly in their character with the barrier reef; separated, that is, by a relatively shallow channel from the land, but facing the sea with an almost perpendicular wall which rises from a very great depth.

Finally, in many cases, especially among the single reefs, which taken together constitute the great Australian barrier, there is no trace of any central island; but a circular reef, usually having an opening on its leeward side, stands out in the midst of the sea. These reefs, apparently unconnected with other land, are what are called "Atolls."

How have these barrier reefs, encircling reefs, and atolls been formed? It is certain that the fabricators of these reefs cannot live at a greater depth than in the fringing reefs. How can they have grown up, then, from a thousand

fathoms or more? Why do they take so generally the circular form? What is the connexion, finally, between fringing reefs and atolls? The only thoroughly satisfactory answer to these questions has been given by Mr. Darwin, from whose beautiful work on Coral Reefs I have borrowed most of the foregoing details. Consider for a moment what would be the effect of a slow and gradual submergence of the island of Mauritius—a submergence, perhaps, of a few feet in a century (at any rate, not greater than the rate of upward growth of coral) continued for age after age. As the edge of the fringing reef sank, new coral would grow up from it to the surface; and, as the most active and important of the reef-builders flourish best in the very surf of the breakers, so the margin of the reef would grow faster than its inner portion, and the discrepancy would increase as the latter, sinking deeper and deeper, became further removed from the region of active growth. Nevertheless, the sea-bottom within the reef would constantly tend to be raised by the accumulation of fragments, and by the deposit of fine mud, in its sheltered and comparatively calm waters. On the other hand, on the seaward face of the reef, no possible extension could take place by direct growth; and that by accumulation must be exceedingly slow, the incessant wash of tides, waves, and currents tending incessantly to spread any talus over a wider and wider area.

Thus, then, the edge of the reef unceasingly compensates itself for the depression which it undergoes, while, inside the reef, only a partial compensation takes place, and, outside, hardly any at all. Continue the sinking process until its highest peak was but a few hundred feet above the surface, and all that would be left of Mauritius would be an island surrounded by an encircling reef; carry on the depression further still, and a circular reef, or atoll, alone would remain. But the region of the coral reefs is, for the most part, that of constant winds. During the whole process of growth of the reef, therefore, one of its sides—that to windward—has been exposed to more surf

than that to leeward. Not only will the greater quantity of *débris*, therefore, have been heaped up by storms upon the windward side, but the coral builders themselves will here have been better fed, better aerated, and consequently more active. Hence it is that, other things being alike, there is a probability that the leeward side of the reef will grow more slowly, and repair any damages less easily, than the windward side; and hence, again, as a result, the known fact, that the practicable channels of entrance into encircling reefs or atolls are usually to leeward.

The winds and waves are singularly aided in grinding down the corals into mud and fragments, by the *Scari* and *Holothuriæ* which haunt the reefs; the former browsing upon the living Polypes with their hard and parrot-like jaws, and passing a fine calcareous mud in their excrements; the latter, more probably, swallowing only the smaller fragments and mud, and, having extracted from them such nourishment as they may contain, casting out a similar product. It is curious to reflect upon the similarity of action of these wormlike *Holothuriæ* upon the sea-meadows of coral, to that which the Earthworms, as Darwin has shown, exert upon our land meadows!

In the Palæozoic period, reefs like those which have just been described appear to have abounded in our own latitudes; and there is the most striking superficial resemblance between the ancient beds of calcareous rock which record their existence, and the masses of coral limestone, hard enough to clink with a hammer, which are now being formed in the Pacific, by the processes of accumulation of coral-mud and fragments, and their consolidation by percolating water. Closer examination, however, shows an important difference in the nature of the corals which compose the two reefs. The modern limestones are made up of *Perforata*, Millepores, and *Aporosa*. The ancient ones contain Millepores, but usually neither *Perforata* nor *Aporosa*,—both these groups being replaced by the *Rugosa*, none of whose members (with some doubtful exceptions) have survived the Palæozoic period. On the other hand, *Palæocyclus* and

Pleurodictyon are the only genera, belonging to the *Aporosa* or *Perforata*, which have yet been discovered in strata of greater than mesozoic age.

The CTENOPHORA.*—These are freely swimming marine animals, which never give rise by gemmation to compound organisms, and are always of a soft and gelatinous consistence, their chief bulk being made up by the greatly developed mesoderm. Many are oval or rounded (*Beröe, Pleurobrachia*, Fig. 31), while in others the body is produced into lobes (*Callianira*), or may even be ribbon-shaped (*Cestum*); but, whatever their form, they present a distinct bilateral symmetry, similar parts being disposed upon opposite sides of a median plane, which is traversed by the axis of the body. The mouth is situated at one end of this axis, which may be termed the oral pole. At the opposite, or aboral pole, there is no median aperture, but usually, if not invariably, a pair of apertures a short distance apart. The faces of the halves of the body present four longitudinal bands of long and strong cilia, disposed in transverse rows, like so many paddles; these constitute the chief organs of locomotion. Each half is also often provided with a long retractile tentacle; and lobed processes of the body, or non-retractile tentacula, may be developed on its oral face. The mouth leads into a wide, but flattened, gastric sac, the aboral end of which is perforated, and leads into a chamber termed the *infundibulum*. From the aboral face of this, a canal which bifurcates, or two canals, lead to the aboral apertures. On opposite sides of the infundibulum a canal is given off towards the middle of each half of the body, which sooner or later divides into two, and these two again subdivide, so that four canals, which diverge and radiate towards the inner faces of the rows of paddles, are

* Allman ('Monograph of the Tubularian Hydroids,' 1871, p. 3) considers that the *Ctenophora* are more properly arranged among the *Hydrozoa*. I confess, however, that I see no reason to depart from the conclusion to which I was led by the study of the structure of *Pleurobrachia*, many years ago, that the *Ctenophora* are peculiarly modified *Actinozoa*.

eventually formed. Having reached the surface, each radiating canal enters a longitudinal canal, which underlies the row of paddles, and may give off branches, or unite with the other longitudinal canals in a circular canal at the aboral end of the body. In addition, two other canals, which run parallel with each flat face of the gastric sac, open into the infundibulum. And, when retractile tentacula are present, their cavities also communicate with the same chamber.

The entire system of canals is in free communication with the gastric cavity, and corresponds with the enterocœle of an *Actinia*. Indeed, an *Actinia* with only eight mesenteries, and these exceedingly thick, whereby the intermesenteric chambers would be reduced to canals; with two aboral pores instead of the one pore, which exists in *Cereanthus;* and with eight bands of cilia corresponding with the reduced intermesenteric chambers, would have all the essential peculiarities of a Ctenophoran.

The question whether the *Ctenophora* possess a nervous system or not is still under debate. Between the aboral apertures there is a rounded cellular body, on which there is seated, in many cases, a sac containing solid particles, like one of the lithocysts of the medusiform *Hydrozoa*. I see no reason to doubt that the rounded body is a ganglion and the sac a rudimentary auditory organ. Bands which radiate from the ganglion to the rows of paddles may be regarded as nerves; though they may contain other than nervous structures.*

* Grant originally described a nervous ganglionated ring, whence longitudinal cords proceeded in *Cydippe* (*Pleurobrachia*), but his observation has not been verified by subsequent investigators. According to Milne-Edwards, followed by others (among whom I must include myself), the nervous system consists of a ganglion, situated at the aboral pole of the body, whence nerves radiate, the most conspicuous of which are eight cords which run down the corresponding series of paddles; and a sensory organ, having the characters of an otolithic sac, is seated upon the ganglion. Agassiz and Kölliker, on the other hand, have denied that the appearances described (though they really exist) are justly interpreted. And again, though the body, described as an otolithic sac, undoubtedly exists in the position indicated in all or most of the *Ctenophora*, the question has been raised whether it is an auditory or a visual organ.

These problems have been re-

The ova and spermatozoa are developed in the lateral walls of the longitudinal canals, which correspond with the faces of the mesenteries in the *Coralligena*, and the sexes are usually united in the same individual.

The development of the *Ctenophora* has recently been thoroughly investigated by Kowalewsky and by A. Agassiz ('Memoirs of the American Academy of Arts and Sciences,' 1874).

Fig. 31.

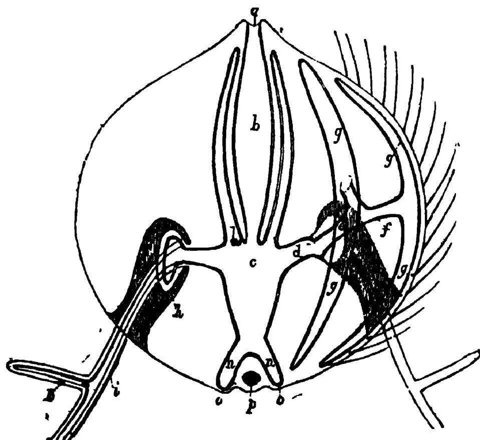


Fig. 31.—Diagram of *Pleurobrachia*.—*a*, Mouth; *b*, stomach; *c*, infundibulum; *d*, horizontal canal; *e*, one of its branches dividing again at *f* into two branches which open into the longitudinal canals, *gg*, parallel with which the ciliated area runs; *h*, sac of the tentacle, *i*, with one of its branches, *k*; *l*, canal running by the side of the stomach; *m*, tentaculigerous canal; *nn*, canals opening at the aboral apertures, *o*, on each side of *p*, the ganglion and lithocyst.

The laid egg is contained in a spacious capsule, and consists of an external thin layer of protoplasm, which, in some cases, is contractile, investing an inner vesicular substance.

cently reinvestigated with great care, and by the aid of the refined methods of modern histology, by Dr. Eimer, whose description of the nervous system has already been quoted (*supra*, p. 64).

After fecundation, the vitellus thus constituted divides into two, four, and finally, eight masses; on one face of each of these the protoplasmic layer accumulates, and is divided off as a blastomere of much smaller size than that from which it arises. By repeated division. each of these gives rise to still smaller blastomeres, which become distinctly nucleated when they have reached the number of thirty-two, and form a layer of cells, which gradually spreads round the large blastomeres, and invests them in a complete blastodermic sac. At the pole of this sac, on the face opposite to that on which these blastoderm cells begin to make their appearance, an ingrowth or involution of the blastoderm takes place, which, extending through the middle of the large yelk-masses towards the opposite pole, gives rise to the alimentary canal. This, at first, ends by a rounded blind termination; but from it, at a later period, prolongations are given off which become the canals of the enterocœle.

At the opposite pole, in the centre of the region corresponding with that in which the cells of the blastoderm first make their appearance, the nervous ganglion is developed by metamorphosis of some of these cells.

The invaginated portion of the blastoderm, which gives rise to the alimentary canal, appears to answer to the hypoblast, while the rest corresponds with the epiblast. The large blastomeres which become enclosed between the epiblast and hypoblast in the manner described, seem to serve the purpose of a food-yelk; and the space which they originally occupied is eventually filled by a gelatinous connective tissue, which possibly derives its origin from wandering cells of the epiblast.

In those *Ctenophora* the bodies of which depart widely from the globular form in the adult state, the young undergo a sort of metamorphosis after they leave the egg, and have acquired all the essential characters of the group to which they belong.

As might be expected from their extreme softness and perishable nature, no fossil *Ctenophora* are known.

CHAPTER IV.

THE TURBELLARIA, THE ROTIFERA, THE TREMATODA, AND THE CESTOIDEA.

THE TURBELLARIA.—The animals which constitute this group inhabit fresh and salt water and damp localities on land. The smallest are not larger than some of the *Infusoria*, which they approach very closely in appearance, while the largest may attain a length of many feet. Some are broad, flattened, and discoidal, while others are extremely elongated and relatively narrow. None are divided into distinct segments, except the genus *Alaurina*, in which there are four; and the ectoderm, which constitutes the outer surface of the body, is everywhere beset with vibratile cilia. Rod-like bodies, similar to those met with in some *Infusoria* and in many *Annelida*, are often embedded in its substance, and in some genera (*e.g.*, *Microstomum*, *Thysanozoon*) true thread-cells occur. Stiff setæ project from the ectoderm in some species.

The aperture of the mouth is sometimes situated at the anterior end of the body, sometimes in the middle, or towards the posterior end, of its ventral face. In many, the oral aperture is surrounded by a flexible muscular lip, which sometimes takes on the form of a protrusible proboscis.

A definite digestive cavity can hardly be said to exist in the lowest *Turbellaria* (*e. g. Convoluta*) in which the endodermal cells are not arranged in such a manner as to bound a central alimentary cavity, and the food finds its way through the interstices of an endodermal parenchyma. In the higher forms, the alimentary cavity, which may be simple or ramified, provided with an anal aperture or without one,

is lined by the endoderm, between which and the ectoderm is an interspace more or less completely occupied by the connective and muscular tissues of the mesoderm. Hence there is no definite perivisceral cavity.

The *Turbellaria* possess vessels of two kinds. 1. *Water vessels*, which open externally by one or more pores, and are ciliated. When these vessels are present, there are usually two chief lateral trunks, from which many branches are given off. It is probable that the ultimate ends of these branches open into lacunar interspaces between the elements of the tissues of the mesoderm. 2. *Pseud-hæmal vessels*, which appear to form a closed system, usually consisting of one median dorsal and two lateral trunks, which anastomose anteriorly and posteriorly. The walls of these vessels are contractile and not ciliated, and their contents are clear, and may be coloured. These two systems of vessels have been shown by Schulze to co-exist in *Tetrastemma*. The nervous system consists of two ganglia placed in the anterior end of the body, from which, in addition to other branches, a longitudinal cord extends backwards on each side of the body. In some cases, these lateral trunks exhibit ganglionic enlargements, from which nerves are given off; and they may become approximated on the ventral side of the body, thereby showing a tendency to the formation of the double ganglionated chain characteristic of higher worms. Most possess eyes, and some have auditory sacs. The *Turbellaria* are both monœcious and diœcious, and the reproductive organs vary from the utmost simplicity of structure to considerable complexity. In most, the embryo passes by insensible gradations into the form of the adult, but some undergo a remarkable metamorphosis.

The *Turbellaria* are divisible into two groups. In the one, the *Aprocta*, the digestive cavity is cæcal, having no anal aperture; in the other, the *Proctucha*, it is provided with an anal opening. The two groups form parallel series, in each of which organisation advances, from forms which are little more than gastrulæ provided with reproductive organs, to

animals of relatively high organisation. In the simplest of the *Aprocta*, such as *Macrostomum*,* the oral opening is devoid of any protrusible muscular proboscis, and the alimentary sac is a simple straight bag. The male and female generative organs are united in the same individual, and each consists of an aggregation of cells; which, in the former case, gradually enlarge, fill with yelk-granules, and become ova; while, in the latter, they are converted into spermatozoa. The generative cells are contained within a sac, which opens externally by a median pore on the oral face of the body, the male aperture being posterior to the female. The margins of the male aperture are produced into a curved prominence, the penis.

Those *Turbellaria* which resemble *Macrostomum* in having a straight, simple digestive cavity, are termed *Rhabdocœla*. They, for the most part, possess a buccal proboscis, which is capable of being protruded from, or retracted into, a chamber formed by the walls of the circum-oral region of the body (Fig. 32, *o*).

In some (*e.g. Prostomum*) the anterior end of the body is provided with a second hollow muscular proboscidiform organ, which may be termed the *frontal proboscis*.

In all the higher rhabdocœlous *Turbellaria*, the female generative apparatus becomes complicated by the presence of a special gland, the *vitellarium* (Fig. 32, *m*), in which an accessory vitelline substance is formed. There is a single or double *germarium* (Fig. 32, *l*), having nearly the same structure as the ovary of *Macrostomum*, and the ova are formed in it in the same way. When detached, however, they contain no vitelline granules; but the two vitellaria, which are long and simple or branched tubes, open into the oviduct; and the vitelline matter which they secrete envelopes the proper ovum, and becomes more or less fused with it, as it passes into the uterine continuation of the oviduct connected with the outer, or vaginal, end of the uterus. There is usually a spermatheca, or receptacle for the seminal fluid (Fig.

* E. Van Beneden, 'Recherches sur la Composition et la Signification de l'Œuf,' 1870, p. 64.

32, *k*), and the eggs, after impregnation, are enclosed within a hard shell (Fig. 32, *n*). The testes and vasa deferentia

Fig. 32.



Fig. 32.—*Opisthomum* (after Schulze).—*a*, Central nervous system; ramifications of the water vessels are seen close to it; *b*, mouth; *c*, proboscis; *d*, testes; *e*, vasa deferentia; *f*, vesicula seminalis; *g*, penis; *h*, sexual aperture; *i*, vagina; *k*, spermatheca; *l*, germarium; *m*, vitellarium; *n*, uterus with two ova enclosed within their hard shells.

(Fig. 32, *d*, *e*) generally have the form of two long tubes. The penis is often eversible and covered with spines (Fig. 32, *g*).

In some genera a difference is observed between the eggs produced in summer, which have a soft vitelline membrane, and those produced later. These so-called *winter ova* have hard shells.

The water-vascular system consists of lateral trunks, which open by a terminal pore, or by many pores, and give off numerous ramifications. They are not contractile, but their inner surface is ciliated.

Many of the *Rhabdocœla* multiply by transverse fission; and, in the genus *Catenula*, the incompletely separated animals produced in this way swim about in long chains.

The vitellus of the impregnated ovum undergoes complete yelk-division, and the embryos pass directly into the form of the parent; but the precise nature of the steps of the developmental process require further investigation. However, there seems little reason to doubt that the ectoderm and endoderm are formed by delamination.

In the remaining *Aprocta*, termed *Dendrocœla*, the digestive cavity gives off many cæcal, frequently branched, processes into the mesoderm, one of which is always median and anterior (Fig. 33); and the mouth is always provided with a proboscis. Some (*Procotyla*) have a frontal proboscis, and others (*Bdellura*) a posterior sucker. The animals commonly known as *Planariæ* belong to this division. Some are marine, some fresh-water, and some terrestrial.

In the fresh-water forms, the female reproductive apparatus has a distinct vitellarium, as in the higher *Rhabdocœla*, and there is only one common genital aperture. But, in the marine *Planariæ* (Fig. 33), there is no vitellarium; the ovaries and testes are numerous, and scattered through the mesoderm, being connected with the exterior by ramifications of the oviducts and of the vasa deferentia. A ramified gland, which secretes a viscid albumen or envelope for the eggs, opens into the vagina, and the female is distinct from the male aperture. *Planaria dioica* is unisexual.

In some of the *Planariæ* there are distinct water-vascular

canals of the ordinary kind; but in the land Planarians* two nearly simple canals, occupied by a spongy tissue, and

Fig. 33.

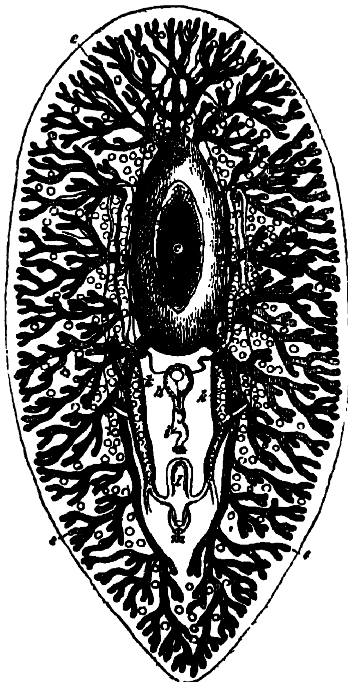


Fig. 33.—*Polycelis* (*Leptoplana*) *lævigata* (after Quatrefages).—*a*. mouth; *b*, buccal cavity; *c*, œsophageal orifice; *d*, stomach; *e*, ramifications of gastric cæca; *f*, ganglia; *g*, testes; *h*, vesiculæ seminales; *i*, male genital canal and penis; *k*, oviducts; *l*, spermathecal dilatation at their junction; *m*, vulva.

the connexion of which with the exterior has not been observed, occupy the place of the water vessels.

* Mosely, "On the Anatomy and Histology of the Land Planarians of Ceylon." (Philosophical Transactions, 1873.)

The fresh-water *Planariæ*, like the *Rhabdocœla*, undergo no metamorphosis in the course of their development; and the like is true of some of the marine *Dendrocœla*. Keferstein * has carefully worked out the development of *Leptoplana* (*Polycelis*). The vitellus undergoes division first into two and then into four equal blastomeres; next, from one surface of these four blastomeres, four small segments are, as it were, pinched off. These divide rapidly, and form a blastoderm, which grows over the more slowly dividing large segments, and eventually encloses them. So far, the process is very similar to that which has been described in the *Ctenophora*. But though Keferstein describes and figures the various stages by which the globular ciliated embryo attains the form of the adult, neither his description nor the figures enable one to say whether the alimentary cavity arises by delamination or by invagination, nor to trace the mode of origination of the buccal proboscis, though this organ is one of the first to make its appearance, and its aperture becomes the future mouth.

In some of the marine *Planariæ*, however, the embryo, when it leaves the egg, differs very widely from the adult. Johannes Müller described such a larva, in which the body is provided with eight lobes or processes, one ventral and median in front of the mouth, three lateral, and one dorso-median. The edges of these processes are fringed by a continuous series of cilia, which pass from one process on to another, so as to form a complete circlet round the body. The successive working of the cilia forming this lobed transverse girdle of the body produces the appearance of a rotating wheel, as in the *Rotifera*. The eyes are situated on the aboral face of the embryo, in front of the ciliated circlet, while the mouth opens immediately behind it. As development proceeds, the lobes disappear, and the body takes on the ordinary Planarian character.

* 'Beiträge zur Anatomie und Entwickelungsgeschichte einiger See-Planarien,' 1868.

As will be seen, some of the *Proctucha* have larvæ

Fig. 34.

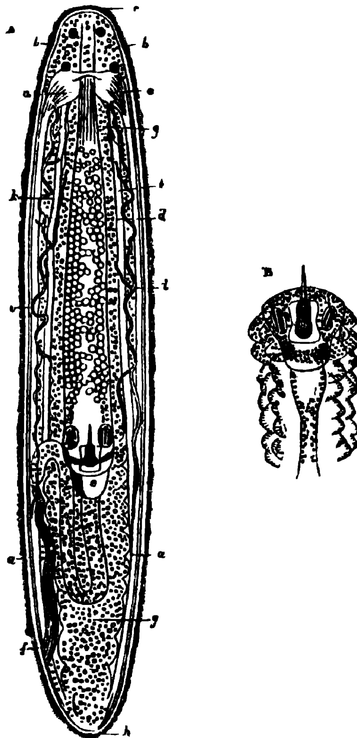


Fig. 34. A.—Young *Tetrastemma*.—*aa*, central ganglia of the nervous system; *bb*, ciliated fossæ; *c*, aperture through which the proboscis is protruded; *d*, anterior portion of proboscis; *e*, posterior muscular part, fixed to the parietes at *f*; *g*, intestine; *h*, anal aperture; *i*, water-vessels; *k*, rhythmically contracting vessels. (After Schulze.) B. Anterior extremity of the everted proboscis of *Tetrastemma*, exhibiting the principal and the reserve stilets. (After Schulze.)

similarly provided with a præ-oral ciliated zone; and larvæ

of the same fundamental type abound among the polychætous *Annelida*, the *Echinodermata*, and the *Mollusca*.

The lowest *Proctucha*, such as *Microstomum*, have no frontal proboscis (whence they are termed *Arhynchia*), and they differ very little from the lowest *Rhabdocœla*, save in the fact that there is an anus, and that the sexes are distinct. But all the other *Proctucha* (*Rhynchocœla*, or Nemerteans) are provided with a frontal proboscis, which sometimes occupies the greater part of the length of the body (Fig. 34). It has special retractor muscles, and its internal surface is either merely papillose, or may possess a peculiar armature, consisting of a sharp chitinous style (Fig. 34, B). There is no buccal proboscis, but the mouth leads into a long, straight intestine, with short, lateral, cæcal dilatations.*

The *Proctucha* usually present only the pseud-hæmal vessels, though, as has been mentioned above, Schulze found water-vessels co-existing with them in *Tetrastemma* (Fig. 34).

The nervous system of the *Proctucha* is like that of the *Aprocta*; but, in correspondence with the often extreme elongation of the body, the backwardly-prolonged cords are very stout. Moreover, the ganglia are united by an additional commissure over the proboscis, which thus traverses a nervous ring. In some, the lateral cords approach one another on the ventral aspect of the body, and ganglionic enlargements appear where the nerves are given off, thus presenting an approximation to the double ganglionated chain of higher forms.

In addition to eyes, almost all the *Proctucha* possess two ciliated fossæ, one on each side of the head (Fig. 34, *bb*), which receive nerves from the ganglia. Occasionally two otolithic vesicles are attached to the cerebral ganglia.

The *Proctucha* are almost always diœcious. The simple reproductive glands are lodged in the intervals between the saccular dilatations of the intestine, and the ova and spermatozoa usually make their way out by the dehiscence of

* For the organisation of the Rhynchocœle *Turbellaria*, or Nemerteans, see Dr. C. McIntosh's elaborate monograph lately published by the Ray Society.

the integument. In some, however, the embryos are developed in the ovarian sacs, or in the cavity of the body. In most of the *Proctucha*, the egg, after passing through the morula stage, acquires an alimentary cavity,

Fig 35.

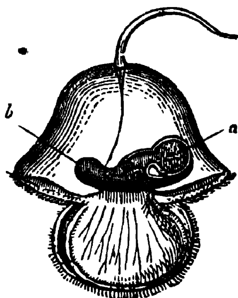


Fig. 37.



Fig. 36.

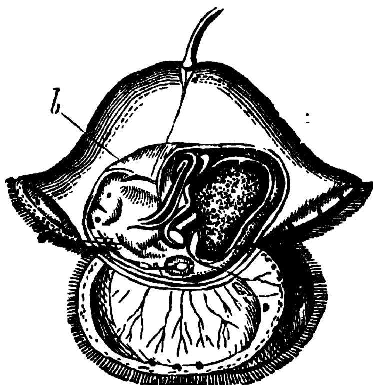


Fig. 35–37.—*Pilidium gyrans* (after Leuckart and Pagenstecher.)
35. Young *Pilidium; a*, alimentary canal; *b*, rudiment of the Nemertean.
36. *Pilidium* with a more advanced Nemertean.
37. Newly-freed Nemertean.

apparently by delamination, and passes, without other metamorphosis than the shedding of a ciliated outer investment, into the form of the adult.

Professor A. Agassiz* has described a free-swimming larva, the broad anterior end of the body of which is surrounded by a zone of cilia, immediately behind which the mouth opens; while, around the anal aperture, at the narrow posterior end, is a second circlet of cilia. This larva exactly resembles those forms of polychætous Annelidan larvæ which are called *Telotrocha*. As in these Annelids, the region of the body which lies between the two ciliated rings elongates and becomes segmented, while a pair of eyes and two short tentacles are developed on the head in front of the præ-oral ciliated band. But, as development advances, the segmentation becomes obliterated, the ciliated bands and the feelers vanish, and the worm assumes the characters of a Nemertean.†

In species of the genus *Lineus*, the ciliated embryo which leaves the egg is speedily converted into a body like a helmet with ear-lappets, and having a tuft of cilia in place of a plume (Fig. 35). The lappets are fringed with long cilia, and between them, where the head would fit into a helmet, is the aperture of a mouth, which leads into a cæcal pouch-like alimentary cavity. This larva was named by Muller, who discovered it, *Pilidium gyrans*. On each side of the ventral face of the *Pilidium*, two involutions of the integument take place. Aggregations of cells in relation with these, and probably forming part of the mesoblast, appear, eventually enclose the alimentary canal of the *Pilidium*, and give rise to an elongated vermiform body, in which the characteristic features of a Nemertean soon become discernible (Fig. 36). The worm thus developed becomes detached (Fig. 37) and falls to the bottom, carrying with it the alimentary canal of the *Pilidium*, and leaving the ciliated integument to perish.

In this remarkable process of development the formation

* "On the Young Stages of a few Annelids." (Annals of the Lyceum of New York, 1864.)

† It is very probable, however, that this larva belongs to the genus *Polygordius*, which appears to be an annectent form between the *Turbellaria* and other groups. See Schneider, "Ueber Bau und Entwickelung von Polygordius." ('Archiv für Anat. und Physiologie,' 1868.)

of the Nemertean body may be compared, on the one hand, to that of the segmented mesoblast in *Annelida* and *Arthropoda*, and, on the other, to that of an Echinoderm, (especially *Echinus*,) within its larva.

The ROTIFERA.—The "wheel-animalcules," as they were termed by the older observers, on account of the appearance of rotation produced, as in many Annelid larvæ, by the working of the vibratile cilia with which the oral end of the body is provided, were formerly included among the *Infusoria*. However, they are true *Metazoa*, as their vitellus undergoes division into blastomeres, and the tissues of the body are produced by the metamorphosis of the cells into which the blastomeres are converted. They are free or adherent, but never absolutely fixed animals, and they do not multiply by gemmation or fission. The oral end of the body is usually broader than the opposite extremity, and presents the form of a disk, sometimes produced into tentacle-like prolongations (Fig. 39). The edges of this *trochal disk* are fringed with long cilia, but the general surface of the body, instead of being ciliated, as in the *Turbellaria*, is formed by a dense, generally chitinous, cuticular layer, which is sometimes converted into a kind of shell and variously sculptured. Transverse constrictions, which are slight in the anterior part of the body, but may become more marked towards its posterior end, give rise to an imperfect segmentation. The segments do not appear to exceed six, and the divisions are less marked in the tubicolous than in the free *Rotifera*. The mouth is a funnel-shaped cavity, situated in the middle, or on one side, of the trochal disk. The walls of this cavity are abundantly ciliated, and at the bottom is a muscular pharynx, or *mastax*, provided with a peculiar armature. Sometimes, as in *Stephanoceros*, a large crop-like cavity lies between the mouth and the mastax, and the aperture of communication between this crop and the mouth is guarded by a valve formed by two broad membranous folds which project into the cavity of the crop. The armature of the mastax

generally consists of four pieces—two lateral, the *mallei*, and two central, constituting the *incus*. The contraction of the muscular masses, to which the mallei are attached, causes the free ends of the latter to work backwards and forwards upon the incus, and crush the prey which is taken into the mouth.*

A short œsophagus, provided with cilia or vibratile membranes, leads into a digestive cavity bounded by the endoderm. The anterior or gastric part of this cavity is usually dilated, and gives off a large cæcum on each side. The posterior, narrower, intestinal part usually opens externally by a cloacal chamber; but, in some Rotifers (*e.g. Notommata*), the alimentary cavity is a blind sac, devoid of intestine or anus; and in the males, so far as they are known, the whole alimentary canal is aborted and represented by a solid cord.

A spacious perivisceral cavity occupies the interval between the walls of the alimentary canal and the parietes of the body. The latter contains circular and longitudinal muscular fibres, which may be smooth or striated.

Opening into the cloaca there is usually a large thin-walled vesicle with rhythmically contractile walls; and, in connexion with this, are two delicate water-vessels, which pass forwards, often giving off short lateral branches, and eventually break up into numerous ramifications in the trochal disk. The branches are open at the ends, whereby the cavities of the water-vessels are in communication with the perivisceral cavity on the one side, and with the surrounding water on the other. Here and there, in the course of the main trunks and at the ends of the branches, long cilia, which, by their constant undulation, give rise to a flickering motion, are situated.

The nervous system is represented by a relatively large single ganglion placed on one side of the body, near the trochal disk. One or more eyespots are sometimes seated

* See, for the various forms of this apparatus, Gosse, "On the Structure, Functions, and Homologues of the Manducating Apparatus in the *Rotifera*." (Phil. Trans. 1855.)

on the ganglion, and there are other organs which appear to be sensory. Such are the ciliated pit and the spur-like process (*calcar*) or processes, provided at the end with a tuft of setæ, which occur in many Rotifers, and are more or less closely connected with the ganglion. In some there is a sac filled with calcareous matter (otocyst?) attached to the ganglion.

Fig. 38.

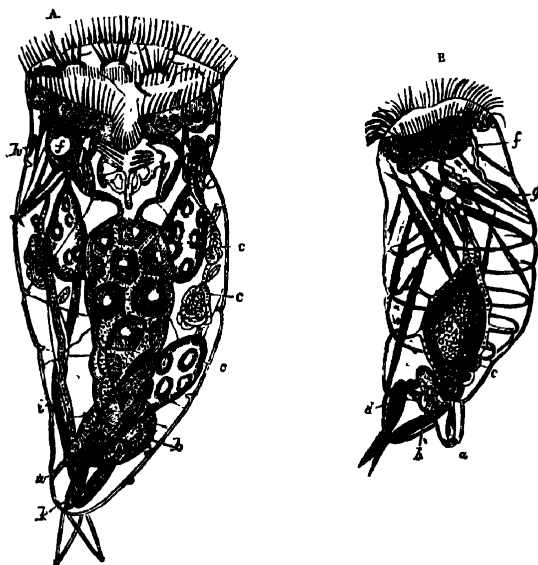


Fig 38.—*Hydatina senta* (after Cohn).—A, female: *a*, anus; *b*, contractile vesicle; *c*, water vessels; *e*, ovary; *f*, ganglion. B, male: *a*, penis; *b*, contractile vesicle; *c*, testis; *f*, ganglion; *g*, setigerous pit.

The ovarium and the testis are simple glands which open into the cloaca, and are always placed in distinct individuals. All the males at present known differ from the females in being much smaller, and in their digestive canal being arrested in its development. The males copulate with the

females, and the eggs are sometimes attached to, and carried about by, the latter—*e.g. Brachionus.*

In some Rotifers, the eggs are distinguishable, as in certain *Turbellaria*, into *summer* and *winter ova*. The latter are enclosed in a peculiar shell. In *Lacinularia*, it appeared to me that the winter ova were segregated portions of the ovarium, and that they were probably developed without impregnation. Cohn, on the contrary, has given reasons for believing that the summer ova are occasionally, if not always, developed without fecundation, and that it is the winter ova which are fecundated.

The egg undergoes complete yelk-division, and the embryo gradually passes into the adult form. The blastomeres are soon of unequal sizes, and the smaller, as an epiblast, invest the larger, which form the hypoblast.

Salensky's * recent observations on *Brachionus urceolaris* show that a depression arises on one face of the epiblast and that the antero-lateral parts of this depression are converted into the trochal disk, while its median posterior part grows out into the "foot;" and he points out the resemblance of the embryo in its early stages to that of some Gasteropods.

An involution of the epiblast at the bottom of the depression gives rise not only to the oral chamber, but also to the mastax; eventually communicating with the gastro-intestinal division, which is developed out of the hypoblast. The ganglion is a product of the epiblast.

Some of the modifications of the general structure thus described which occur in the different groups of the *Rotifera* are of considerable interest.

Thus, in the tubicolous forms, the body is elongated and terminated posteriorly by a discoidal surface of adhesion. The animals (of which a number are often associated together), fixed by this disk, enclose themselves in cases, the foundation of which is a gelatinous secretion. The intestine is bent upon itself (*Lacinularia*, Fig. 39, II.), and opens upon the face of the body opposite to that upon which the

* 'Zeitschrift für Wiss. Zoologie,' 1872.

ganglion is placed. The peduncle of attachment is therefore a process of the neural face of the body. In these *Rotifera* the trochal disk is sometimes produced into long ciliated tentacula, which surround the mouth symmetrically (*Stephanoceros*—Fig. 39, V.) or its edges may be provided with two circlets of cilia, one in front of, and the other behind. the oral aperture; and it may be bilobed or horseshoe-shaped, as in *Melicerta* and *Lacinularia** (Fig. 39, I. II.).

In the free Rotifers, the body may be rounded, sac-like, and devoid of appendages, as in the genus *Asplanchna*,

Fig. 39.

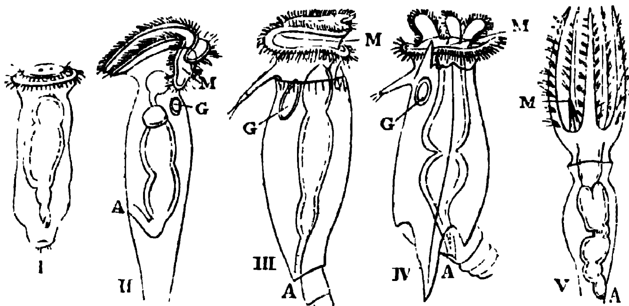


Fig. 39.—Diagrams showing the arrangement of the cilia of the trochal disk in the *Rotifera*. I. Larval *Lacinularia*. II. Adult *Lacinularia*. III. *Philodina*. IV. *Brachionus*. V. *Stephanoceros*. M, mouth; G, ganglion; A, anus.

which has neither anus nor intestine. In *Albertia* and *Lindia*, on the other hand, the body is elongated and vermiform. Most of the free *Rotifera* (Fig. 38) are provided with a segmented and sometimes telescopically-jointed "foot," usually terminated by two styles, which can be approximated or divaricated like pincers, and serve to anchor the body. This foot is a median process of that face of the body which is opposite to that on which the ganglion is placed, so that

* Huxley, *Lacinularia socialis*. (Transactions of the Microscopical Society, 1851.)

it is not the homologue of the peduncle of the tubicolous forms.

Polyarthra and *Triarthra* possess long, symmetrically arranged, movably articulated setæ; and *Pedalion* has median appendages proceeding from both the neural and the opposite faces of the body, as well as lateral appendages.

In most of the free Rotifers the trochal disk is large; it may be bilobed or folded upon itself (Fig. 39, III.), or its surface may give rise to ciliated processes (Fig. 39, IV.). In *Albertia* and *Notommata tardigrada*, however, the trochal disk is reduced to a small ciliated lip around the oral aperture; and there is no trochal disk in *Apsilus*, *Lindia*, *Taphrocampa*, and *Balatro*. Some few Rotifera are parasitic. Thus *Albertia* is an entoparasite, and *Balatro* an ectoparasite, upon oligochætous Annelids.

Under the name of *Gasterotricha*, Metschnikoff and Claparède * include the curious aquatic genera *Chætonotus*, *Ichthydium*, *Chætura*, *Cephalidium*, *Dasyditis*, *Turbanella*, and *Hemidasys*, the last of which alone is marine. These animals have been united with the *Rotifera*, but they differ from them in the absence of a mastax and in the disposition of the cilia, which are restricted to the ventral surface of the body. It appears probable that they form an annectent group between the *Rotifera* and the *Turbellaria*, which last approach the *Rotifera* by such forms as *Dinophilus*.

The free Rotifers present marked resemblances to the telotrochous larvæ of Annelids. The young *Lacinularia*, for example, has a circular præ-oral disk provided with two eye-spots and a second circle of cilia behind the mouth, and is wonderfully like an Annelid larva (Fig. 39, I.). The appendages of *Triarthra* and *Polyarthra* may be compared to the lateral bundles of long setæ of the larvæ of *Spio* and *Nerine*, and the pharyngeal armature is essentially Annelidan. On the other hand, in the sessile tubicolous *Rotifera*, the trochal disk assumes the characters of the lophophore in the *Polyzoa*, and of the tentacular circlet of the Gephyrean

* Claparède and Metschnikoff, 'Beiträge zur Kenntniss der Entwickelungsgeschichte der Chaetopoden,' 1868.

Phoronis. Many years ago I drew attention to the points of resemblance between the *Rotifera* and the larvæ of Echinoderms ("On *Lacinularia socialis*," *l. c.*) Of any such close and direct relations with the *Crustacea*, I see no evidence; but *Pedalion*,* with its jointed setose appendages and curious likeness to some *Nauplius* conditions of the lower *Crustacea*, suggests that connecting links in this direction may yet be found.† In fact, the *Rotifera*, as low *Metazoa* with nascent segmentation, naturally present resemblances to all those groups, which, in their simpler forms, converge towards the lower *Metazoa*.

The TREMATODA.—These are all parasitic, either upon the exterior (ectoparasites) or in the internal organs (endoparasites) of other animals. Many are microscopic, and none attain a length of more than an inch or two. Most have a broad and flattened form, one face being ventral and the other dorsal, and the body is never segmented.

In the adult. the ectoderm is not ciliated, but its outermost layer is a chitinous cuticula. In most *Trematoda*, one or more suckers are developed upon the ventral surface of the body, behind the mouth. These are sometimes armed with chitinous spines or hooks; and setæ of the same character may be developed in other parts of the body, especially in the region of the head.

The mouth is usually terminal, but is sometimes ventral and sub-central; it is ordinarily placed in the centre of a muscular sucker, rarely proboscidiform. The alimentary canal is never provided with an anus. Sometimes a simple

* Hudson, "On a New Rotifer." ('Monthly Microscopical Journal,' 1871.)

† The singular marine genus *Echinoderes* (Dujardin) is perhaps such a link. These are minute wormlike animals, with a rounded head, followed by a number (10 or 11) of distinct segments, the last of which is bifurcated. There are no limbs, but the head is provided with recurved hooks, and the body segments with paired setæ. The nervous system appears to be represented by a single ganglion, which lies in the head and presents eye-spots. The development of *Echinoderes* is unknown. (See Greef, 'Archiv für Naturgeschichte,' 1869.)

sac, it is often bifurcated, and occasionally branched, like that of the dendrocœle *Turbellaria*. Sometimes (*Amphilina, Amphiptyches*) the alimentary canal is absent; and, according to Van Beneden, it becomes aborted in the adult *Distoma filicolle*. The interval between the endoderm and the ectoderm is occupied by a cellular or reticulated mesoderm, in which abundant muscular fibres are developed. The peripheral muscular fibres form an external circular and an internal longitudinal layer.

The water-vascular system is well developed, and may consist of—(1) a contractile sac, which opens externally and communicates with (2) longitudinal vessels with contractile non-ciliated walls, from which proceed (3) non-contractile and ciliated branches which ramify through the body and the ultimate ramifications of which probably end by open mouths, as in the *Rotifera*.

There is no pseud-hæmal system. The nervous system has not been discovered in all; but, when it exists, it has the same arrangement as in the aproctous *Turbellaria*. Eye-spots have been observed, but no other sense-organs. With rare exceptions, the *Trematoda* are hermaphrodite, and the reproductive organs are constructed upon the same type as in the rhabdocœle *Turbellaria*, a large vitellarium being always present. The accessory vitellus is included, in the form of numerous pellets, along with the primitive ovum, and is absorbed *pari passu* with the development of the embryo.

Aspidogaster conchicola (Fig. 40) inhabits the pericardial cavity of the fresh-water mussel; it is a very convenient subject for examination on account of its small size, and the ease with which it can be rendered sufficiently transparent for the display of the arrangement of its internal organs, by the judicious use of the compressorium. The flat oval body, rounded posteriorly, is produced in front into a truncated cone, on the face of which the mouth opens. The ventral sucker is very large, and its surface is subdivided into rectangular areas. There is no perivisceral cavity, its place being occupied by a mass of

spongy cellular tissue. The oral cavity leads into an oval, thick-walled, muscular pharyngeal bulb, whence an elongated pyriform sac, which constitutes the rest of the alimentary canal, is continued. This occupies a great part of the body, and extends nearly to its posterior end; but there is no anus. A contractile vacuole placed at the hinder extremity of the body opens outwards by

Fig. 40.

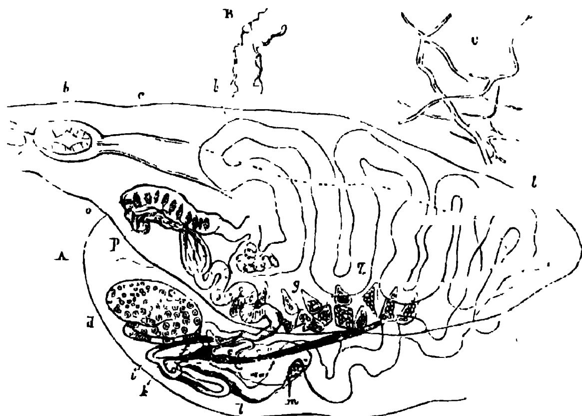


Fig 40.—*Aspidogaster conchicola.*—A, arrangement of the alimentary and reproductive organs; profile of the animal in outline. *a*, mouth; *b*, muscular pharynx; *c*, stomach; *d*, germarium; *e*, internal vas deferens; *f*, common vitellarian duct; *g*, vitellarium; *h*, one of its ducts; *i*, *k*, oviduct; *l*, uterus; *m*, testis; *o*, vagina; *p*, penis, continuous posteriorly with the external vas deferens; B, one of the lateral contractile vessels; C, ramifications of the ciliated vessels.

a small pore (Fig. 41, *a*), and gives off two lateral contractile non-ciliated canals (*b*), which pass to the anterior end of the ventral sucker and there end blindly; but before reaching this termination each gives off a non-contractile ciliated vessel, (Fig. 41, *c*) which, on arriving at the pharynx, turns backwards and ramifies through the body. The cilia diminish towards the extremities of these vessels,—the ter-

minations of the corresponding canals in the *Rotifera* being, on the contrary, richly ciliated. No nerves have as yet been found in *Aspidogaster*.

As in most *Trematoda*, the genitalia (Figs. 40 and 42) form a large part of the viscera, and the structure of the complex hermaphrodite apparatus is in some respects so peculiar, that it is needful to describe it in detail. It consists of—1. The germarium. 2. The vitellarium. 3. The oviduct. 4. The uterus and vagina. 5. The common vestibule. 6. The testis. 7. The vasa deferentia, internal and external.

Fig. 41.

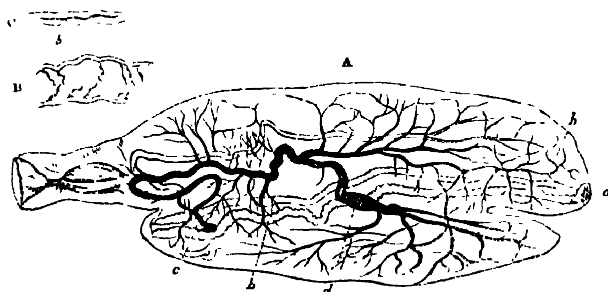


Fig. 41.—A, water-vascular system of *Aspidogaster conchicola*; *a*, terminal pore; *b*, lateral contractile vessels; *c*, lateral ciliated trunks, that of the left side shaded; *d*, dilatation of this trunk; B, one of larger, and C, one of the smaller, ciliated vessels.

8. The penis and its sac. The ovary (*d*) is the anterior of two rounded masses lying in the sucker. At first sight it appears to be oval, but it is, in fact, pyriform, the larger end being anterior, while the posterior narrower extremity is bent backwards beneath the anterior end. Before it reaches the anterior extremity of the mass. however, it is bent sharply back again, parallel with itself, and so passes into the oviduct (Fig. 40, *i*). The ovary is surrounded by a delicate, but strong, coat, enclosing a mass of transparent protoplasm. At the anterior end of the ovary minute granules are scattered through this substance, and are oc-

casionally surrounded by a faint, clear area (Fig. 43, A 1). These are the rudimentary germinal spots and vesicles of the future ova, the course of whose development may be readily traced by working from the anterior to the posterior extremity of the ovary. The germinal spots become larger, and gradually assume the appearance of vesicular nuclei; while the clear area around them in like manner becomes larger, and acquires more and more the appearance of a cavity. While this cavity is small, it has no distinct wall, but, as it enlarges, the contour of the wall becomes distinctly marked (Fig. 43, A 2. 3. 4). On examining the ovary close to the commencement of the oviduct, a division of the homogeneous protoplasmic basis or matrix of the ovary into areas surrounding each germinal vesicle becomes obvious. On the application of pressure, the matrix breaks up into masses corresponding with these areas in size, which are very flexible, but when left to themselves assume a rounded or oval form, and have all the appearance of perfect ova, except that they possess no vitelline membrane, and that the yelk, instead of being granular, is clear, and comparatively small. These *primary ova*, as they may be termed, become detached, and pass into the oviduct. Here they are fecundated, and, becoming surrounded by a great mass of accessory yelk, and a shell, gradually acquire the appearance of the complete ova.

The accessory yelk is the product of the vitellarium—a large double gland consisting of a number of oval, pyriform, or irregular granular masses placed on each side, at the junction of the sucker with the body (Fig. 40, *g*).

These masses appear to be quite independent of one another; nor do they at first present any obvious communication with the genitalia; but if the oviduct, just after it becomes free from the ovarium, be examined, it will be found to receive a short duct (Fig. 42, *f*), filled with strongly refracting granules of the same nature as those in the vitellarium. This duct is enlarged posteriorly, and then divides into two ducts filled with the same matter, which take a direction towards the vitellarium, but can be traced no

further than they contain granules (Fig. 42). By the careful application of pressure, however, the granules may be forced from the vitellarium, through an anterior and posterior branch upon each side, into these ducts.

The oviduct (Fig. 42, *i*) is richly ciliated internally; it is at first applied to the under surface of the ovarium, and when it becomes free it receives a canal (*e*), which may be traced back to the testis, and which would appear

Fig. 42.

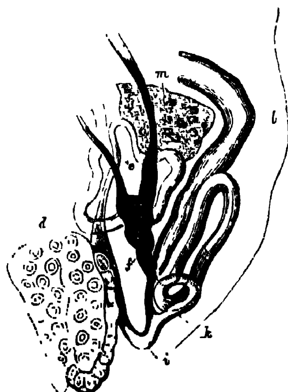


Fig. 42.—*Aspidogaster conchicola.*—Reproductive organs on a larger scale. Letters as in Fig. 40. The commencement of the external vas deferens is seen behind the vitellarian ducts.

to correspond with the internal vas deferens of other *Trematoda* described by Von Siebold.* This canal, however, presents no dilatation, or internal vesicula seminalis. The oviduct next receives the duct of the vitellarium, and then becoming much convoluted (*k*), and rapidly widen-

* The connection of this duct with the testis in the *Trematoda* has recently been denied by Stieda ('Müller's Archiv,' 1871). I had no doubt of its existence in *Aspidogaster*, but I have had no opportunity of re-examining this animal since the publication of Stieda's paper.

ing, passes into the uterus (*l*), a wide tube, which runs forwards, disposed in many undulating curves (Fig. 40, *l*), to terminate on the left side of the anterior part of the body, close to the male organs. Posteriorly, the walls of the uterus are thin; but in its anterior, or vaginal, part they become thick and muscular. The genital vestibule into which the vagina opens is very small.

The testis (*m*) is an oval body of the same size as the ovarium, and situated just behind it. Minute water-vessels ramify upon it, as upon the ovarium; and it contains a granular and cellular mass, but no spermatozoa. The external vas deferens (Figs. 40 and 42) is a delicate duct, which passes forwards and comes into contact with the ovarium, without, however, so far as I could observe, communicating with it or with the oviduct; it then bends backwards and upwards, passing between the anterior vitellarian masses into the fore part of the body. Here it suddenly becomes about twice as wide as before, and runs forwards, as an undulating thick tube, to the penis (Fig. 40, *p*), a short and conical body, occupying the bottom of a large pyriform sac, which opens in common with the uterus. The spermatozoa are linear.

The development of the ova presents many very interesting peculiarities (Fig. 43). Above the junction of the duct of the vitellarium with the oviduct the contents of the latter were pale and clear, and presented no formed particles beside the primary ova which had just been detached from the ovarium (Fig. 43, C). Below the insertion of the vitellarian duct, however, the oviduct was full of granules like those in the vitellarium, mixed up with ova in a more advanced state. In the smallest of these (Fig. 43, D), the shell of the ovum had commenced, but was incomplete at one end. At the opposite extremity, it enclosed a mass of irregularly aggregated vitelline granules, which covered almost one-half of a round pale mass, not larger than one of the primary ova; in which, however, three nuclei (two of which were very close together, as if they had just divided) were to be distinguished. In more advanced ova the shell was

complete, but either colourless or of a very pale brown hue. In some of these the primary ova contained many nuclei and were imbedded in and surrounded by, a confused mass of accessory yelk granules; while in others these granules were aggregated into a number of regular spheroidal masses (Fig. 43, B).

As development proceeds, the accessory yelk-masses gradually disappear; the primitive ovum, now become the ho-

Fig. 43.

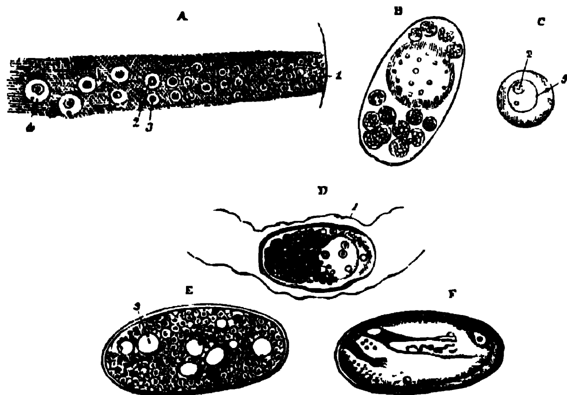


Fig. 43.—*Aspidogaster conchicola*.—A, section of the ovary; 1, its anterior end; 2, germinal spot surrounded by a distinct wall; 3, 4, a complete germinal vesicle and spot; C, a primary ovum; D, young state of a complete ovum: the primary ovum partially surrounded by yelk granules and a shell; B, complete ovum, with the accessory yelk aggregated into spheroids; E, vacuolated embryonic mass; F, embryo.

mologue of the blastodermic disk or vesicle in other animals, to all appearance increasing at their expense. At the same time, clear rounded vacuoles in various numbers appear in its substance; but the nuclei of the germ, though very minute, can, with proper care, be readily detected between these. In the final stages the shell becomes browner, the vacuoles and granules disappear, and the substance of the embryo appears homogeneous. But if carefully examined,

the minute nuclei become visible, especially if water be allowed to act on the tissue, and, if the shell be burst, and its contents poured out, they readily break up into small but well-marked cells, each with its nucleus. At the same time, the embryo takes on a form not very distantly resembling that possessed by the adult; into which it eventually passes without any metamorphosis.*

Thus it appears that, in *Aspidogaster*, the ovarium gives rise to primary ova, which pass down the oviduct and become fecundated, either by the spermatozoa conveyed by the internal vas deferens, or by those received by the vagina when copulation with another individual or, possibly, self-impregnation, occurs; that, next, the essential part of the process of "yelk-division" takes place, the germinal spot dividing and subdividing, and the primary ovum becoming in this way converted into the spheroidal blastoderm; that, contemporaneously, the blastoderm becomes invested by the accessory yelk granules poured in by the vitellarian duct, and by a shell; that the accessory yelk arranges itself into spheroidal masses, which probably supply the blastoderm with the means of its constant enlargement; and that, finally, the accessory yelk disappears, and the blastoderm becomes converted into the embryo.

The modifications exhibited by other *Trematoda* concern the number of the suckers, of which there are usually several in the ectoparasites, but not more than one in the endoparasites; their support on a chitinous framework, or the addition to them of spines or hooklets, similar to those of *Cestoidea* or *Acanthocephala*: the bifurcation of the intestinal canal, and the ramification of its branches, so that the forms of the alimentary apparatus repeat the two extremes observed in the aproctous *Turbellaria;* the existence of two nervous ganglia with a single transverse commissure

* The substance of this account of the structure and development of *Aspidogaster*, with the illustrative figures, was published in 1856 in *The Medical Times and Gazette*. M. E. van Beneden has recently thrown much light on the mode in which the ova of the *Trematoda* are formed and developed in his 'Recherches sur la composition et la signification de l'Œuf.'

in many; and the occasional presence of sensory organs (eye-spots). The non-contractile canals of some genera are destitute of cilia, except at their inner terminations.

The variations of the reproductive organs are rather of position than of structure. Diœcious Trematodes are very rare, the most important being the formidable *Bilharzia*, the male of which is the larger and retains the female in a *gynæcophore*, or canal, which is formed by the

Fig. 44.

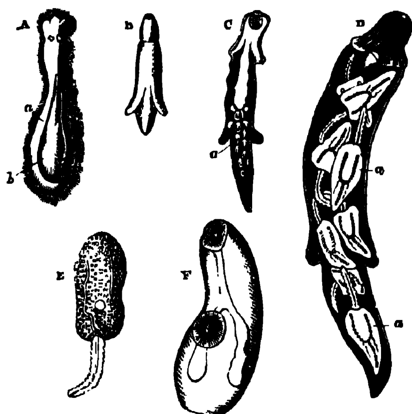


Fig. 44.—A, B, *Monostomum mutabile;* A, the ciliated embryo (*a*) enclosing the zooid, (*b*,) represented free in B (after Siebold); C, *Redia*, or king's yellow worm of *Distoma pacificum*, containing germs of other *Rediæ;* D, *Redia* containing *Cercariæ* (*a*); E, *Cercaria;* F, *Distoma*, which results from the metamorphosis of the *Cercaria.* (After Steenstrup.)

infolding of the margins of the concave side of the body. *Bilharzia* has neither intromittent organ nor seminal pouch, and the history of its development has not been traced beyond the escape of a ciliated embryo from the ovum. This parasite is found in the blood vessels of man, chiefly in those of the urinary organs, the ova escaping from the body through the ulcerated surfaces to which the parent

gives rise. In the ectoparasites, the embryo passes into a form identical with or closely resembling that of the parent while still within the egg, as in *Aspidogaster*. When this happens (*e.g. Distoma variegatum*, *D. tereticolle*), the one end of the embryo is often provided with spines, and it is capable of slow creeping movements. But, in most of the endoparasites, the embryo leaves the parent as a morula, which is usually ciliated. Thus, in *Distoma lanceolatum*, *D. hepaticum*, and *Monostomum mutabile*, the embryo which escapes from the egg has a ciliated investment, which propels it rapidly through the water, and may be provided with eyespots and water-vessels (Fig. 44, A). On becoming attached to the animal upon which it is parasitic, the embryo of *Monostomum* gives exit to a larva, having the form of a cylindrical sac with two lateral prolongations and a tapering tail. The *Redia*, as this form is called (Fig. 44, B, C), has a mouth and a simple cæcal intestine, but no other organs. In its cavity a process of internal gemmation takes place, giving rise to bodies resembling the parent in shape, but destitute of reproductive organs, and furnished with long tails, by which they are propelled. These creatures, called *Cercariæ* (Fig. 44, E), escape by bursting through the *Redia*, and, after a free swimming existence, penetrate the body of some other animal, their tails dropping off. They then become encysted, and, under suitable conditions, assume the adult form, and develope reproductive organs (Fig. 44, F).

The cycle of forms through which *Distoma militare* passes has been nearly completely traced, and may be briefly stated as follows. 1st. The parent form, whose habitat is the intestines of water-birds, bears on its anterior extremity two alternating circles of larger and smaller hooklets, and a few others, irregularly disposed. Rings of papillæ give the centre of the body an annulated aspect. The mouth, almost terminal, leads into the long straight digestive cæcum. The generative organs are similar to those of *Aspidogaster*; the testes are, however, double, and lack the internal vas deferens. The ova are few, eight or ten in number.

2nd. From each ovum issues a ciliated larva, showing the rudiments of, 3rd, a *Redia*, but the mode of development of the latter has not been fully traced. The perfect *Redia* is found attached to the body of a water snail (*Paludina*), the ciliated investment having disappeared. It consists of a sac, within which is suspended a tubular bag, containing coloured masses, probably alimentary. Anteriorly, the head is represented by a kind of crown, in which no œsophagus exists as yet, and not far from the posterior extremity the two lateral projections, characteristic of Distomatous *Rediæ*, appear. During the rapid growth of the zooid, the head becomes marked off by a constriction, and a mouth and gullet, with a pharyngeal dilatation, admit aliment to the digestive sac. In the body cavity, external to this sac, vesicles appear, rapidly increase, and take the form of *Cercariæ*; the *Redia* bursts, and these new zooids are set free. 4th. The *Cercaria* has a long tail with lateral membranous expansions, by means of which it swims after the fashion of a tadpole. The pharyngeal bulb is followed by an œsophagus, which, opposite the ventral sucker, divides; the two branches ending in a cæcum on either side of the contractile vacuoles of the water-vascular system. These are median, the terminal quadrate chamber opening into an anterior circular one, whence are given off the two main canals which traverse the body longitudinally, and are then lost. 5th. After swimming about freely for a while, the *Cercaria* fixes itself upon, or bores its way into, a *Paludina*; the tail dropping off, and the body coating itself with a structureless cyst, in which it remains quiescent, but undergoes some further advances in development, the coronal hooklets making their appearance. 6th. When a *Paludina*, thus infested, is swallowed by a water bird and digested, the cysts are set free in the alimentary canal of the bird; sexual organs appear within the included *Distoma*; the body elongates and narrows anteriorly; the sucker moves nearer the head, and the coronal circlets reach their full development. The *Distoma* gradually assumes the form of the parent, attaches itself by

its hooklets to the intestinal walls, and acquires complete sexual organs.* Thus the developmental stages of *Distoma militare* may be summed up, as: 1. Ciliated larva. 2. *Redia.* 3. *Cercaria.* 4. *Cercaria,* tail-less and encysted, or incomplete *Distoma.* 5. Perfect *Distoma.*

The stages of transition vary in different genera. Thus, several generations of *Rediæ* may intervene between the

Fig. 45.

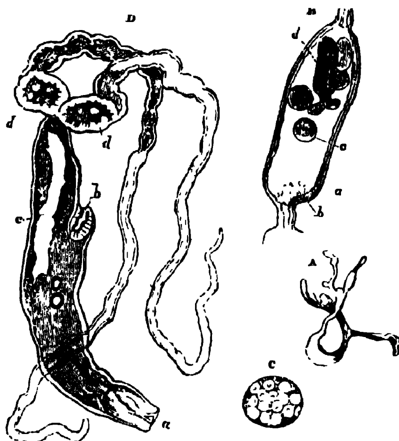


Fig. 45. — *Bucephalus polymorphus* of the fresh-water mussel. A, ramified sporocyst; B, portion of the same more magnified, *a*, outer coat, *b*, inner; *c*, *d*, germ masses in course of development; C, one of the germ masses more highly magnified; D, *Bucephalus*, *a*, *b*, suckers; *c*, clear cavity; *d*, caudal appendages.

third and fourth stages; or the mature animal may appear at the close of this stage, having undergone no Cercarian metamorphosis.

In *Bucephalus polymorphus*, a parasite of the fresh-water mussel (Fig. 45), two caudal appendages, which seem to correspond with the tail of the ordinary *Cercariæ*, become

* Van Beneden, 'Mémoire sur les Vers Intestinaux.'

enormously elongated. They are converted into ramified tubes called *sporocysts*, which sometimes occupy all the interspaces of the viscera of the mussel. These develope new *Bucephali* by internal gemmation. The Trematode condition appears to be the genus *Gasterostomum*, which inhabits fresh-water fishes.

The Sporocysts, Rediæ, and Cercariæ, free or encysted, are found almost exclusively in invertebrated animals, while the corresponding adult Trematodes are met with in the vertebrated animals which prey upon these *Invertebrata*.

The singular double-bodied *Diplozoon paradoxum* has been shown by Von Siebold to result from a sort of conjugation between two individuals of a Trematode, which, in the separate state, has been named *Diporpa*. The *Diporpæ*, when they leave the egg, are ciliated and provided with two eyespots, with a small ventral sucker and a dorsal papilla. After a time the *Diporpæ* approach, each applies its ventral sucker to the dorsal papilla of the other, and the coadapted parts of their bodies coalesce. They acquire fully developed sexual organs only after this union.*

Gyrodactylus multiplies agamically by the development of a young Trematode within the body, as a sort of internal bud. A second generation appears within the first, and even a third within the second, before the young *Gyrodactylus* is born.

The CESTOIDEA.—The Tape-worms are all endoparasites, and, in their adult condition, infest the intestines of vertebrated animals.

The simplest form known is *Caryophyllæus*,† found in fishes of the Carp tribe. It has a slightly elongated body, dilated and lobed at one end, so as to resemble a clove,

* Zeller, "Untersuchungen über die Entwickelung des Diplozoon paradoxum." ('Zeitschrift für Wiss. Zoologie,' 1872.)

† See the 'Mémoire sur les Vers Intestinaux,' 1858, by M. P. J. van Beneden, to which I am much indebted for information respecting this and other genera of *Cestoidea* which have not fallen under my own observation. Also Leuckart, 'Die Menschlichen Parasiten,' 1863; and Cobbold, 'Entozoa.'

whence the name of the genus. In structure it resembles a Trematode, devoid of any trace of an alimentary canal, but provided with the characteristic water-vascular system and with a single set of hermaphrodite reproductive organs.

In *Ligula*, the body is much elongated, and, at the head end, exhibits two lateral depressions. It is not divided into segments, but there are numerous sets of

Fig. 46.

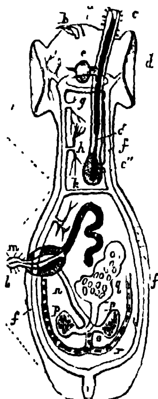


Fig. 46.—Diagram of the structure of a Cestoid worm, with only one joint. The position of the hooks of a *Tænia*, and of one of the proboscides of a *Tetrarhynchus* is indicated. A, head and neck; B, segment of the body corresponding with a *proglottis*; *a*, *rostellum*; *b*, rostellar spines (*Tænia*); *c*, *c'*, *c''*, spinose eversible proboscis (*Tetrarhynchus*); *d*, sucker; *e*, ganglion (?); *f*, lateral, and *g*, circular water vessel; *h*, ramifications of the water vessels; *k*, anastomosing trunk; *i*, contractile vacuole; *l*, genital vestibule; *m*, penis and vas deferens; *n*, vagina, *o*, common cavity and *vesicula seminalis interior*; *p*, ovary; *q*, uterus; *r*, vitellarian duct.

sexual organs arranged in longitudinal series. The openings of the genital glands are situated in the middle line of the body. These parasites inhabit Fishes and Amphibians, as well as water birds, but they attain their sexual state only in the latter.

In the more typical *Cestoidea* the body is elongated, and

presents, at one end, a head provided with suckers, and very generally with chitinous hooks, either disposed circularly around the summit of the head, or upon proboscidiform tentacles, which can be retracted into, or protruded from, the head. Sometimes the head is produced into lobes; and very generally, when lobes or tentacles exist, they are four in number, and are disposed symmetrically round the head. A short distance beyond the latter, the slender body widens and becomes transversely grooved, so as to be marked out into segments. Longitudinal water-vessels run parallel with one another through the body, and are connected by transverse trunks in each segment, and by a circular vessel in the head. In *Bothriocephalus latus,* the principal trunks are occupied by a spongy reticulated tissue.

In most of the tape-worms, innumerable, solid, strongly refracting corpuscles are scattered through the substance of the body (Fig. 48, A). It is probable that these are more or less calcified connective tissue corpuscles. Similar bodies which occur in some *Trematoda* were found by Claparède to be lodged in dilated ends of the water-vessels, but it would appear that they are not so situated in the *Cestoidea.**

The distance between these transverse grooves, and their depth, increase towards the hinder end of the body; and each segment is eventually found to contain a set of male and female organs. The genital organs are constructed upon the same general plan as those of the *Trematoda*, but the uterus, as it fills with ova, usually takes the form of a ramified sac. At the extreme end of the body, the segments become detached, and may for some time retain an independent vitality. In this condition each segment is termed a *proglottis;* and its uterus is full of ova.

The embryo is developed in these ova in the same way as in the *Trematoda;* and, as in the latter group, it may either be ciliated (as in *Bothriocephalus*) or non-ciliated, which

* Sommer and Landois, "Ueber den Bau der geschlechtsreifen Glieder von *Bothriocephalus latus.*" ('Zeitschrift für Wiss. Zoologie,' 1872.) Leuckart, however, maintains the contrary opinion, 'Die Menschlichen Parasiten,' p. 175.

it is the more usual case. The embryo is a solid morula, on one face of which four or six chitinous hooks, disposed symmetrically on either side of a median line, are developed.

If the egg is placed in appropriate conditions, the hooked embryo emerges from the shell, and rapidly increases in size. After a time, a cavity appears in the midst of the cells of which the morula is composed, and a chitinous cuticula is developed upon the outer surface of the embryo. Ramified water-vessels make their appearance in the wall

Fig. 47.

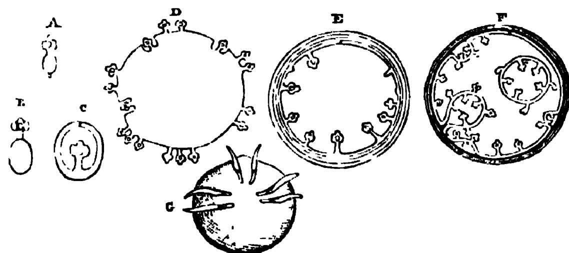


Fig. 47.—Diagrams illustrative of the relation between *Tænia*, *Cysticercus*, *Cœnurus*, and *Echinococcus*.—A, B, young *Tæniæ* in the *Scolex* stage, the latter with an enlarged *receptaculum Scolicis*, into which the head and neck are withdrawn in C, *Cysticercus*; D, *Cœnurus*; E, hypothetical condition of *Echinococcus*, in which "*Tænia* heads" are developed only on the inner surface of the primary cyst; F, *Echinococcus* with secondary cysts; G, embryo *Tænia* (after Stein).

of the spheroidal sac thus formed, and in some cases open by an external pore. There is, therefore, a very close resemblance between this cestoid embryo and the sporocyst of a Trematode.

When the saccular embryo has attained a certain size, a thickening and invagination take place, usually at one (*Tænia*), sometimes at many (*Cœnurus*, *Echinococcus*), points of its wall. The invagination of the wall elongates inwards, and becomes a cæcum, the cavity of which opens outwards. At the bottom of the interior of this cæcum, and therefore

on what is morphologically its external surface, the hooks of those species which possess them are developed, while, upon the side-walls, elevations arise, which become converted into suckers. The cæcum is next evaginated or turned inside out, and the embryo has the form of a phial, of

Fig. 48.

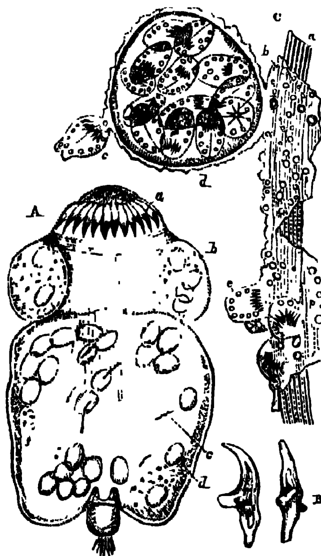


Fig. 48.—*Echinococcus veterinorum.*—A, "Tænia head," or *Scolex;* *a*, hooks; *b*, suckers; *c*, cilia in water vessels; *d*, oval, strongly refracting particles, B, single hooks; C, portion of the elastic cyst, *a*; with the inner membranous primary cyst, *b*; *c* and *e*, *Scolices* developing from its inner surface; *d*, a secondary cyst.

which the evaginated cæcum forms the neck. Round its apex are the hooks, and below these the suckers, forming a complete Cestoid head; while the sac answers to the body of the phial. The original hooks of the embryo are cast off in the course of this process.

If the eggs of the Tape-worm have passed into the alimentary canal of an animal in which the worm is unable to attain its sexual condition, the hooked embryo, as soon as it is hatched, bores its way through the walls of the alimentary canal, and eventually becomes lodged in the connective tissue between the muscles, or in the liver, or in the brain or eye. Here it goes through the changes which have been described, and, generally, the sac undergoes very great dilatation. The region of the wall of the sac to which the cestoid head is attached becomes invaginated, and thus is enclosed within a chamber, the parietes of which are really constituted by the outside of its own body. In this condition, the animal is what is termed a *Cystic worm*, or bladder-worm; and when there is only one head it is a *Cysticercus*. In the genera *Cœnurus* and *Echinococcus* the cystic worm has many heads; and, in *Echinococcus*, the structure of the cystic worm is still further complicated by its proliferation, the result of which is the formation of many bladder-worms enclosed one within the other, and contained in a strong laminated sac or *cyst*, apparently of a chitinous nature, secreted by the parasite (Fig. 48).

In the Cystic condition, the Tape-worms never acquire sexual organs; but, if transported into the alimentary canal of their appropriate hosts, the heads become detached from the cysts, and, rapidly growing, give rise to segments, which become sexual *proglottides*. The Tape-worms are rarely met with in both the cystic and cestoid conditions in the [illegible] animal; but the cystic form is found in some creature which serves as prey to the animal in which the cestoid form occurs. Thus:—

CYSTIC FORM.	CESTOID FORM.
Cysticercus cellulosæ. (Muscles of the Pig)	*Tænia solium.* (Man)
Cysticercus —— ? (Muscles of the Ox)	*Tænia mediocanellata.* (Man)
Cysticercus pisiformis. (Liver of the Rabbit)	*Tænia serrata.* (Dog, Fox)

CYSTIC FORM.	CESTOID FORM.
Cysticercus fasciolaris. (Liver of Rats and Mice)	*Tænia crassicollis.* (Cat)
Cœnurus cerebralis. (Sheep's brain)	*Tænia cœnurus.* (Dog)
Echinococcus veterinorum. (Liver of Man and of domestic Ungulata)	*Tænia Echinococcus.* (Dog)

The embryo of *Tænia cucumerina* passes, in the body of the Dog-louse (*Trichodectes canis*), into a *Cysticercoid*, or minute unjointed and sexless Tænia, without any terminal dilatation. The dog devours the louse and the Cysticercoid becomes a *Tænia cucumerina* in his intestine. The eggs of the *Tænia*, contained in fæces adherent to the hair of the dog, are in turn devoured by the louse, and thus the "vicious circle" of parasitism is maintained.

The cystic *Tetraphyllidea* frequent osseous fishes, their sexual maturity being attained in the bodies of Plagiostomes. The head is provided with four suckers, or lobes, which may be stalked and unarmed, as in *Echeneibothrium*, or furnished with hooklets as in *Acanthobothrium*; while, in *Tetrarhynchus*, four proboscidiform tentacles, thickly set with hooklets, are retracted into sheaths alongside of the suckers (Fig. 46).

The *Diphyllidea* have two suctorial disks, two armed rostellar prominences, and a collar of hooklets on the neck.

The migrations of the *Pseudophyllidea* are chiefly from fishes and amphibians to water birds, one genus (*Bothriocephalus*) containing species which enter the human body, probably in the flesh of fresh-water fishes. The head has neither suckers nor lobes, but is deeply grooved on either side. In *Bothriocephalus* the genital apertures are in the middle of each segment. The embryo is ciliated, and swims actively in water. Recent experiments tend to show that the development of the embryo in this genus may take place directly, or without the intervention of a *Cysticercus* stage.

It is obvious that the *Cestoidea* are very closely related to the *Trematoda*. In fact, inasmuch as some of the latter are anenterous, and some of the former are not segmented, it is impossible to draw any absolute line of demarcation between the two groups. It would appear that the *Cestoidea* are either Trematodes which have undergone retrogressive metamorphosis and have lost the alimentary canal which they primitively possessed; or that they are modifications of a Trematode type, in which the endoderm has got no further than the spongy condition which it exhibits in *Convoluta* among the *Turbellaria*, and in which no oral aperture has been formed; or lastly, it is possible that the central cavity of the body of the embryo *Tænia* simply represents a blastocœle.

If the *Cestoidea* are essentially Trematodes, modified by the loss of their digestive organs, some trace of the digestive apparatus ought to be discoverable in the embryo tapeworm. Nevertheless, nothing of the kind is discernible, unless the cavity of the saccular embryo is an enterocœle. And if this cavity is a blastocœle, and not an enterocœle, it may become a question whether the tape-worms are anything but gigantic morulæ, so to speak, which have never passed through the gastrula stage.

CHAPTER V.

THE HIRUDINEA, THE OLIGOCHÆTA, THE POLYCHÆTA. THE GEPHYREA.

THE HIRUDINEA.—The Leeches are aquatic or terrestrial, more or less distinctly segmented, vermiform animals, most of which suck blood, though some devour their prey. The ectoderm is a cellular layer, covered externally by a chitinous cuticula, and except in *Malacobdella*, devoid of cilia. Very commonly it is marked by transverse constrictions into rings, which are more numerous than the true *somites*, as indicated by the ganglia and the segmental organs; and simple glands may open upon its surface. One or more suckers, which serve as organs of adhesion, are developed upon it. In some (*Acanthobdella*) bundles of setæ are present; in others (*Branchellion*) the sides of the body are produced into lobe-like appendages; but none have true limbs, unless the lateral appendages of *Histriobdella* are to be considered as such; nor are the anterior segments of the body so modified as to give rise to a distinct head.

The mouth is generally situated at the anterior end of the body; the anus at the opposite extremity, on the dorsal side of the terminal sucker. The buccal cavity may be armed with several serrated chitinous plates, as in the Medicinal Leech, where there are three such teeth. By their aid the Leech incises the skin and gives rise to the well-known triradiate mark of a leech-bite. The buccal cavity usually opens into a muscular, sometimes protrusible, pharynx, from which a narrow œsophagus leads into a stomach, which is frequently produced into lateral cæca. In the Medicinal

Leech (Fig. 49), for example, there are eleven pairs of such cæca, increasing in length and capacity from before backwards. From the stomach a narrow intestine leads to the anus. In *Malacobdella* the alimentary canal is a simple tube bent several times upon itself. The alimentary canal is lined by the cells of the endoderm, and the space between them and the ectoderm is occupied by the mesoderm, which contains abundant connective and muscular elements, and is excavated by the blood-channels, which sometimes have the form of wide sinuses, but in other cases are comparatively narrow vessels with definite walls.

In the lower *Hirudinea*, as *Clepsine*, the sinuses and vessels appear to form one continuous system of cavities containing a fluid which must be regarded as blood. But in the Leech, a distinct pseudhæmal vascular system has attained a great degree of definition and complexity: it consists of (1) a median dorsal trunk; (2) a median ventral trunk, in which the ganglionic nerve-chain lies; (3, 4) two wide lateral longitudinal trunks (Fig. 50). These anastomose with one another, and give off numerous branches, which open into a rich capillary net-work, situated in the muscular layer of the mesoderm,

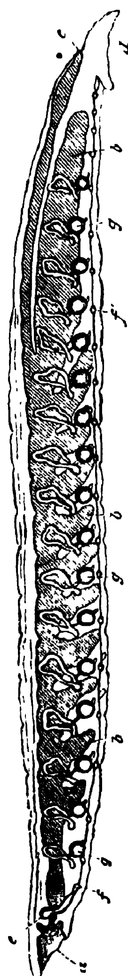


Fig. 49.

Fig. 49.—A longitudinal and vertical section of the body of the Leech (*Hirudo medicinalis*), after Leuckart*—*a*, the mouth; *b*, *b*, *b*, sacculations of the alimentary canal; *c*, the anus; *d*, the terminal sucker; *e*, the cerebral ganglia; *f*, *f*′, the chain of post-œsophageal ganglia; *g*, *g*, *g*, the segmental organs.

* 'Die Menschlichen Parasiten,' 1863.

and on the segmental and reproductive organs. The fluid contained within these vessels has a red colour, and contains no corpuscles.

More or fewer of the segments of the body are provided

Fig. 50.

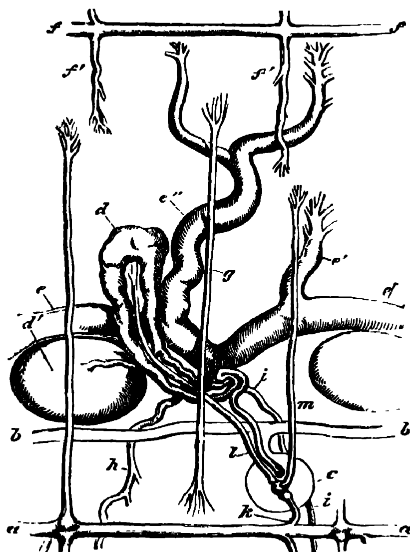


Fig. 50 —A diagrammatic view of the arrangement of the principal vessels of the leech (*Hirudo medicinalis*), after Gratiolet. The inner surface of a portion of one-half of the body is depicted: *a*, *a*, the ventral trunk; *e*, *e'*, *e''*, the lateral trunk and its branches; *f*, *f'*, the dorsal trunk and its branches; *g*, the slender transverse trunks which branch out at each end; *h*, *i*, the transverse ventral branches of the lateral trunk; *k*, *l*, the branch to the testis (*c*), and the segmental organ (*d*); *m*, branch from the dilatation on the testis to the parietal plexuses; *b*, *b*, vas deferens.

with what are termed *segmental organs*. These are tubes which open externally on the ventral wall of the body, while at their other extremities they either open into the sinuses by ciliated mouths (*Clepsine*), or form a closed

and more or less reticulated non-ciliated coil (*Hirudo*). These obviously answer to the ciliated water-vessels of the *Turbellaria* and *Trematoda*.

The nervous system consists of a cerebral mass in front of the mouth, proceeding from which, on each side, is a commissure connecting it with a ventral cord on which ganglia, corresponding in number with the somites of the body, are developed. In *Malacobdella*, these cords are lateral and wide apart, but, in all the other *Hirudinea*, they come close together behind the mouth, and occupy the middle line of the ventral face of the body. In the Leech, according to Leuckart, there are originally thirty pairs of post-oral ganglia, but the seven posterior and the three anterior pairs coalesce, so that only twenty-three pairs are distinguishable in the adult. Nerves are given off to the pharynx and intestines, and the former develope special ganglia.

Simple eyes are usually present on the anterior or oral segment, and receive nerves from the supraœsophageal ganglia. In the Leech these eyes are situated in the first three segments. Cup-shaped depressions of the integument of the anterior segments of the body, lined by peculiar glassy cells and in relation with nerves which terminate in fine filaments, have been discovered by Leydig in several of the *Hirudinea*.*

The elongated spindle-shaped muscle-cells of the body are abundant, and are disposed in a superficial circular, and deep longitudinal layer, while dorso-ventral bands pass from the dorsal to the opposite body-wall.

Malacobdella and *Histriobdella* are diœcious, but the other *Hirudinea* are hermaphrodite. The male organs consist of numerous testicular sacs, situated on each side of the body, and connected by a vas deferens, which usually opens into a sac, terminating in an eversible penis. The spermatozoa are often enclosed in a case or *spermatophore*. The female organs, much smaller than the male, consist of ovaries, with oviducts opening into a vagina. The vaginal orifice is behind that of the penis. In the Leech the eggs

* 'Archiv für Anatomie und Physiologie,' 1861.

are enclosed in a sort of cocoon, formed by a viscid secretion of the integument.

The observations of Rathke and Leuckart on the development of *Nephelis*, *Clepsine*, and *Hirudo* show, that, after the division of the vitellus into a few equal-sized large blastomeres, small blastomeres are separated from the large ones (as in the *Ctenophora* and *Polycelis*), and the rapidly multiplying small blastomeres form an investment to the slowly-dividing large ones. This investment is the epiblast, and becomes the ectoderm, while the included larger blastomeres are eventually converted into the cells of the endoderm. At one end of the body the oral aperture appears, in some cases (*e.g.* *Nephelis*) surrounded by a raised lip, as in the embryo Planarian; and the embryo passes into the Gastrula stage. The body now elongates and, on the ventral face, the mesoblast makes its appearance as a layer of cells, sometimes divided into two longitudinal bands, separated by a median interval. Three pairs of segmental organs, which have only a temporary existence and have been regarded as primordial kidneys, are developed at the posterior end of the body. The mesoblast next becomes divided transversely into the number of somites of which the body is eventually composed; the division first making its appearance on the ventral face of the body. A pair of ganglia, probably derived from the epiblast, is developed in each segment.

Thus, in the Leeches, the segmentation of the body is the result of the segmentation of the mesoblast, which becomes the mesoderm of the adult. And it is this segmentation of the mesoblast, and consequently of the mesoderm, which constitutes the most important difference between the Leech on the one hand, and the Turbellarian and Trematode on the other.

On the other hand, in the development of a mesoblast which undergoes division into segments, the Leeches exhibit the fundamental character of all such segmented Invertebrates as the chætophorous *Annelida* and the *Arthropoda*.

The OLIGOCHÆTA.—The Earthworm (*Lumbricus*) and fresh-water worms (*Nais, Tubifex, Chætogaster*), which are included under this name, are closely allied with the Leeches in the essential points of their structure and development, much as they differ from them in habit and appearance.

They have elongated, rounded, segmented bodies, often divided by many superficial transverse constrictions into rings, which, as in the Leeches, may be more numerous than the proper somites. There are no limbs, but each segment is usually provided with two or four sets of longer or shorter chitinous setæ, which are developed and lodged in integumentary sacs. The outermost layer of the ectoderm is a non-ciliated chitinous cuticle.

The mouth is situated close to the anterior end of the body, but a "cephalic lobe" not unfrequently projects beyond it on the dorsal side. The anus is at the opposite extremity of the body, and the straight alimentary tract which connects the two and is lined by the endoderm, is usually divided into a pharyngeal, œsophageal, and gastro-intestinal portion, the latter often being produced laterally into short cæca. The mesoderm presents well-developed transverse, longitudinal, and dorso-ventral muscular fibres, as in the Leeches. It is excavated by a spacious perivisceral cavity, which contains a colourless corpusculated fluid, and is divided by thin but muscular mesenteries, which stretch from the intestine to the parietes, and thus break up the perivisceral cavity into partially separate chambers. In addition, there is a system of pseud-hæmal vessels, like those of the Leeches, provided with contractile walls, and containing a red non-corpusculated fluid. No communication has been ascertained to exist between these vessels and the perivisceral cavity; but there can be little doubt that, as in the case of the Leeches, they must be regarded as a specially differentiated part of the general system of the perivisceral cavity.

In the majority of the segments there are, as in the *Hirudinea*, paired segmental organs; these are ciliated and their inner ends open into the perivisceral chamber.

The nervous system consists of præ-oral or cerebral ganglia, continued backwards, on the ventral aspect of the body, by commissures on each side of the œsophagus into a double chain of closely united post-oral ganglia.

Large tubular fibres are imbedded in the neurilemma of the ganglionic chain on its dorsal face. In the Earthworm there are three of these—one median and two lateral—extending along the whole length of the ventral end, but not into the œsophageal commissures.* The nature of these structures is unknown.

These animals are hermaphrodite. The generative organs are situated in the front part of the body, the male organs being anterior to the female. In the aquatic *Oligochæta* (*Nais*, *Tubifex*) the genital glands have no proper ducts, but the segmental organs of the segments in which they are contained convey the generative products outwards. In the terricolous forms (*Lumbricus*) the vasa deferentia are continuous with the testes, which are very large. The ovaries, on the other hand, are minute solid bodies attached to one of the mesenteries, and the oviducts are separate tubes with funnel-shaped mouths, which open into the cavity of the segment.

In *Nais* and *Chætogaster*, agamic multiplication occurs by the development of posterior segments of the body into zooids, which may remain associated in chains for some time, but eventually become detached and assume the parental form. Schulze has observed that when a *Nais* has divided into an anterior and posterior zooid, the last somite of the former gradually enlarges, and becomes divided into new somites, the anterior of which give rise to a head. A new zooid is thus developed between the previously existing ones. This process is repeated in what was the penultimate, but is now the ultimate somite of the anterior zooid; and again in the penultimate somite when it has, in the same way, become terminal.

* Claparède, 'Histologische Untersuchungen über den Regenwurm,' 1869.

As the Earth-worm is a very accessible subject, it may be useful to the student to be furnished with an account of some of the chief points of its organisation more in detail.

The exterior of the body of an Earthworm (*Lumbricus terrestris, rubellus* or *communis*) shows a number of close-set transverse grooves which divide its body into numerous narrow rings or segments.* The most anterior segment is small and conical, and presents, on its under surface, a depression which is the oral aperture. The anus is at the opposite end of the body. Behind the mouth, the successive segments rapidly attain their average size; but, in a full-grown worm, a part of the body into which more or fewer of the segments between the twenty-fourth and thirty-sixth inclusively (29?–36, *L. terrestris*; 24–29?, *L. rubellus*; 26–32, *L. communis*) enter, is swollen, of a different colour from the rest, provided with abundant cutaneous glands, and receives the name of *cingulum* or *clitellum*.

In the dorsal median line there is a series of small apertures or pores, one for each segment except the most anterior, which lead into the perivisceral cavity; while upon the ventral surface of the anterior part of the body the eight apertures of the organs of generation are situated. Of these, four, situated two on each side, between the ninth and tenth, and the tenth and eleventh segments, are the openings of the *receptacula seminis*. The openings of the two oviducts are on the fourteenth segment; those of the two vasa deferentia on the fifteenth. Besides these, all the segments, except some of the most anterior, exhibit a pair of minute openings appertaining to the segmental organs; and they are further perforated by the four longitudinal double rows of setæ, which project slightly beyond the surface of the integument, and offer a certain resistance when the worm is drawn from tail to head through the fingers.

The body is invested in a thin and transparent but dense

* The question how far all these segments represent somites may be left open. The history of the development of the Earthworm is in favour of their being true somites.

cuticula, perforated by excessively minute vertical canals. Within this lies a thicker layer, consisting of a reticulated nucleated protoplasm, the meshes of which are filled with a transparent gelatinous substance. This layer probably represents both the *dermis* and *epidermis*, and has been termed the *hypodermis*. Internal to it lies a thick layer of circular muscular bands, in the interstices of which pigment granules occur; and, still more internally, is a much thicker coat of muscular fibres, which are disposed longitudinally.

The cavity circumscribed by this longitudinally fibrous muscular layer is lined by a kind of connective tissue. Corresponding with the divisions between every pair of segments (except in the most anterior part of the body), this connective tissue is continued transversely towards the axis of the body, and passes into that which forms the wall of the intestine; while, on the ventral side, it forms an arch over the ventral nervous cord, and the vessels which accompany it. In the interior of each of these *mesenteric septa*, radiating and circular muscular fibres are abundantly developed, and the former are connected externally with the superficial layer of transverse muscles.

The perivisceral cavity is thus divided into nearly as many short chambers as there are segments; each chamber communicates with the exterior, directly by the dorsal pore and indirectly through the segmental organs, while fluid may pass from one to the other by the supra-neural archways.

The short and curved setæ project much further into the interior of the body than they do on to its exterior. The free apices of each pair are situated close together, while their inner ends diverge from one another. Each is enclosed in a sac in which it is developed, and to which the muscles, by which it is protruded, are attached. There are eight setæ to each somite, one pair not far from the ventral median line on each side; and the other pair placed in the same transverse line, but further outwards.

The mouth leads into a muscular pharynx, with a com-

paratively small internal cavity, which reaches as far back as the seventh segment. From this a narrow œsophagus is continued as far back as the fifteenth or sixteenth segment; and presents three pairs of lateral glandular diverticula, which contain a calcareous matter,* in the region of the twelfth and thirteenth segments. Posteriorly, the gullet opens into a crop, which is succeeded, about the eighteenth segment, by a thickened and muscular gizzard.

Upon this follows the intestine, which has the appearance of a simple tube; but is in reality complicated by the involution of its wall, along the dorsal median line, into a thick fold, which projects into the interior of the intestinal cavity, and is the so-called *typhlosole.* The exterior of the intestine and the cavity of the typhlosole present a coating of yellowish-brown cells.

The *segmental organs* are greatly convoluted tubes, situated one on each side of every segment except the first, and attached to the posterior mesenteric septum of the segment. Each canal communicates internally, by a wide funnel-shaped ciliated aperture, with the perivisceral cavity, while externally, it opens by a minute pore, which is usually close to the internal pair of setæ.†

A colourless fluid, containing colourless corpuscles, and answering to the blood of other invertebrated animals, occupies the perivisceral cavity; but, in addition to this, there is a deep red fluid, devoid of corpuscles, which fills a very largely developed system of pseud-hæmal vessels. These consist of longitudinal and transverse principal trunks, and of very numerous branches which proceed from them and ramify in all parts of the body, except the cuticle and hypodermis.

The longitudinal trunks are three: one *supra-intestinal,* which lies along the dorsal aspect of the alimentary canal; one *sub-intestinal,* which corresponds with this on the

* The nature of this substance has recently been discussed by M. E. Perrier, "Étude sur un genre nouveau des Lombriciens." ('Archives de Zoologie expérimentale,' 1873.)

† Gegenbaur, "Ueber die sogenannten Respirationsorgane des Regenwurms." ('Zeitschrift für Wiss. Zoologie,' 1852.)

ventral aspect of that canal; and one *sub-neural*, which lies beneath the ganglionic cord.

The supra-intestinal and sub-intestinal vessels are connected in the greater number of the segments by pairs of *commissural* transverse trunks, which embrace the intestine, and give off numerous branches to it. The supra-intestinal and sub-neural vessels give off transverse trunks into the mesenteric septa, which branch out into the muscular layers, and some of which anastomose so as to form a second set of transverse communications. Moreover, the sub-neural trunk and the sub-intestinal trunk respectively send branches to each segmental organ, upon which they are distributed, and, anastomosing, give rise to another series of communications between the longitudinal trunks.

In the seven most anterior segments, the longitudinal vessels break up into a network, and there are no distinct transverse commissural vessels. Behind these, and in the region of the generative apparatus, the commissural vessels are greatly dilated, and form from five to eight pairs of so-called *hearts* which are attached to the anterior faces of as many mesenteries. These contract from the dorsal towards the ventral side.

The nervous system consists of two cerebral ganglia lodged above the pharynx in the third segment, and united by commissural cords with the anterior ganglia of the chain, which extends through the whole length of the body on the ventral wall of the perivisceral cavity.

There are no eyes, nor are any other organs of special sense known.

The Earthworm is hermaphrodite. The testes are two pairs of large sacs, each of the anterior pair being bilobed. The testes of opposite sides are united in a common median reservoir, situated in the tenth and eleventh segments, from which, on each side, ducts take their origin. The two ducts of the testes of the same side unite into a single vas deferens, and these two vasa deferentia open externally on the ventral aspect of the fifteenth segment. The ovaries

are two minute solid bodies, not more than $\frac{1}{16}$ of an inch long, attached to the posterior face of the mesenteric septum which separates the twelfth and thirteenth segments. They therefore lie in the cavity of the latter. The oviducts are quite distinct from the ovaries, and open internally by wide funnel-shaped apertures, situated in the cavity of the thirteenth segment. From these funnel-shaped ends the oviducts are continued, as slender tubes, through the mesenteric septum which separates the thirteenth from the fourteenth segment, and open on the ventral face of the latter.

Four globular spermathecæ, or receptacles of the spermatozoa, are situated, two on each side, in the tenth and eleventh segments, and open on the ventral face between the ninth and tenth, and the tenth and eleventh segments respectively. These are filled when copulation takes place, during which process, the two worms are said to be bound together by a tough secretion of their clitella.

The development of the *Oligochæta* has recently been carefully investigated by Kowalewsky. The eggs of the Earthworm are laid in chitinous cocoons or cases, which are probably secreted by the clitella. In addition to the eggs, the cocoons enclose an albuminous fluid, and packets of spermatozoa. The vitellus is invested by a membrane, and contains a germinal vesicle and spot. Complete yelk-division takes place, and eventually the blastocœle becomes reduced to a mere cleft. The blastomeres are disposed in two layers—one consisting of small, and the other of large blastomeres. The embryo thus formed becomes concave on the side formed by the large blastomeres, until it assumes the form of a sac, ciliated externally, with an opening, the future mouth, at one end; the cavity of the sac being the primitive alimentary canal, and the layer of large blastomeres, the hypoblast. Between the two, a mesoblastic layer appears, but the exact manner of its origin is not known. On one face of the saccular embryo the mesoblast becomes divided into a series of quadrate masses, like the protovertebræ of a vertebrate embryo,

disposed symmetrically on each side of a median line, which corresponds with the future ventral median line of the body. Along this line, the epiblast becomes thickened inwards, and the thickening is converted into the ganglionic chain. At the same time, each quadrate mass of the mesoblast is excavated by the development of a cavity in its interior, whereby it becomes converted into a sort of sac. The adjacent anterior and posterior walls of successive sacs unite, and give rise to the mesenteric septa, while their cavities become the chambers of the perivisceral cavity. The segmental organs commence as cellular outgrowths from the posterior face of each septum thus formed, and only subsequently become excavated and communicate with the exterior.

The development of the Earthworm, therefore, closely resembles that of the *Hirudinea*, and more especially that of the Medicinal Leech, in which the digestive cavity of the embryo would seem to be formed, as in the Earthworm, by a process which is, in a sense, invagination. It would appear that the first formed aperture is the mouth; while the anus is a secondary perforation; and the segmentation of the body commences in the mesoblast.

In the fresh-water *Oligochæta*, *Euaxes* and *Tubifex*, the vitellus also becomes divided into large and small blastomeres. The latter extend over the larger blastomeres, and form the epiblast (= ectoderm). A mesoblast (= mesoderm), divided into two broad longitudinal bands, is developed, and the oral cavity is said to be formed by invagination of the epiblast between the anterior ends of the two bands of the mesoblast. In this case, the mouth in these genera is a secondary formation. The innermost layer of large blastomeres becomes the hypoblast (= endoderm).*

The POLYCHÆTA.—Except that the *Polychæta* are almost invariably diœcious and marine, while the *Oligochæta* are

* Kowalewsky, "Embryologische Studien." ('Mem. de l'Acad. de St. Pétersbourg,' 1861.)

monœcious, and inhabitants either of land or fresh water, it is hard to say what absolute characters separate these two groups. The lowest forms of the *Polychœta*, such as *Capitella* and *Polyophthalmus*, might be regarded as marine diœcious *Naidœ*. But, in the higher *Polychœta*, each segment of the body developes lateral processes—the *parapodia*, or rudimentary limbs, which are usually provided with abundant strong setæ; a distinct cephalic segment, the *prœstomium*, appears in front of and above the mouth, and bears eyes and tentacles; while those parapodia which lie in the vicinity of the mouth may be specially modified in form and direction, foreshadowing the jaws of the *Arthropoda*. Ciliated, sometimes plumose, processes of the dorsal walls of more or fewer of the segments may perform the office of external *branchiœ*; and, occasionally, the dorsal surface gives rise to flat shield-like processes, the so-called *elytra*.

The following detailed description of a very common species of *Polynöe*, will give a fair conception of a polychætous Annelid, in which the highest degree of complexity of organisation known in the group is attained:—

Polynöe squamata is an elongated vermiform animal, about an inch long, the body of which is divided into a succession of portions, for the most part similar and equivalent to one another, but presenting peculiar modifications at the anterior and posterior extremities. Each such portion is properly termed a *somite*; while the term "segment" may be retained to indicate generally a portion of the body, without implying its precise equivalency to one somite or to many. Thus, then, the body of the *Polynöe* is composed of a series of twenty-six "somites," terminated anteriorly by a "segment," the *prœstomium* ('Kopf-lappen,' Grube) and posteriorly by another, the *pygidium*, which may or may not represent single somites.

If one of the somites from the middle of the body (Fig. 51, C, D) be examined separately, it will be found to be transversely elongated, so as to be about three times as broad as it is long, and to be slightly convex above and below, presenting a deep, median, longitudinal groove inferiorly.

Laterally the somite is produced into two thick processes, the "*parapodia.*"

Each parapodium divides at its extremity into two portions, a superior and an inferior, which may be denominated re-

Fig. 51.

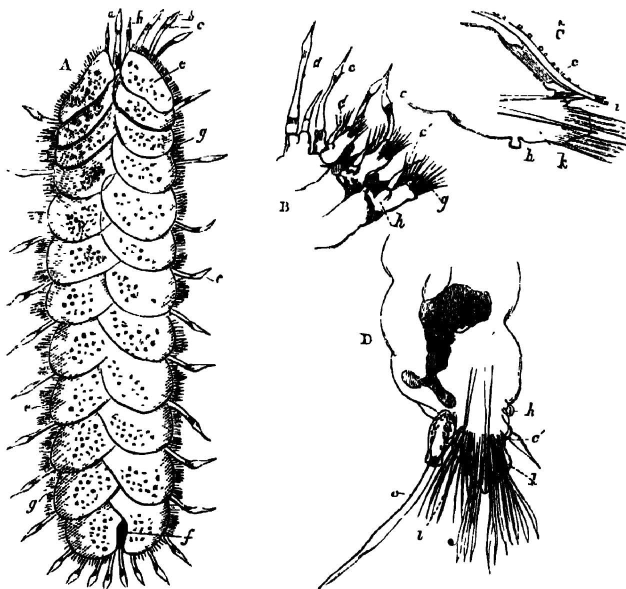


Fig. 51.—*Polynöe squamata.*
A. Viewed from above and enlarged: *a*, *b*, *c*, etc. as in Fig. 53 B; *e*, elytra; *f*, space left between the two posterior elytra; *g*, setæ and fimbriæ of the elytra.
B. Posterior extremity, inferior view: *d*, pygidial cirri; *h*, inferior tubercle; *c*, *c'*, notopodial and neuropodial cirri.
C. Section of half a somite with elytron: *i*, notopodium; *k*, neuropodium.
D. Section of half a somite with cirrus.

spectively the *notopodium* (Fig. 51 *i*) and the *neuropodium* (*k*), the one occupying the "hæmal," or dorsal, the other the "neural" or ventral aspect. The latter is, in this species

so much the larger, that the notopodium appears like a mere tubercle projecting from its upper surface. In other *Annelida*, however, and in the young state of *Polynöe*, the notopodium is as large as the neuropodium. Both divisions of the parapodia are armed with peculiar stiff hair-like appendages (*g*), composed of chitin, and developed within diverticula of the integument, or *trichophores*, in which their bases always remain enclosed. These can be protruded and retracted by muscles attached to their sacs, and they vary exceedingly in form. Three distinct kinds are observable in *Polynöe* alone. The notopodium and the neuropodium carry each a single, sharp, style-like *aciculum*, the greater part of the length of which is imbedded in the parapodium and its divisions, while the point just projects at about the centre of the latter. The neuropodial is very much longer than the notopodial aciculum.

Superiorly, the notopodium carries two transverse rows of more slender organs of a similar nature, the *setæ*: the proximal set are much shorter than the distal, but even the latter do not attain a length of more than $\frac{1}{18}$ of an inch (Fig. 52, G).

The proximal set are somewhat knife-like in shape if viewed in profile, consisting of a comparatively short, straight "handle," by which they are imbedded in their sacs, and of a thick, rounded, curved blade, tapering to a fine point at its extremity. Close-set transverse ridges, finely serrated at their edges, and inclined obliquely to the surface of the blade, traverse its convex anterior circumference, leaving the back free. The distal setæ (Fig. 52, G) have a very similar structure, but they are much elongated and very slender. The handle is longer; and the blade, little curved and simply set on at an angle with the handle, is produced at the end into a long and delicate filament. The base of the blade (E) is beset with incomplete ridges, like those of the short setæ, but towards the middle (F) these ridges appear to encircle the blade completely, assuming the aspect of so many closely imbricated concentric scales, before finally becoming obsolete upon the extremity of the seta.

The neuropodial aciculum needs no special notice, except that the extremity of its trichophore projects as a sort of papilla, less obvious in full-grown specimens, which divides the neuropodium into an upper and a lower portion, the former containing about half as many setæ as the latter.

Fig. 52.

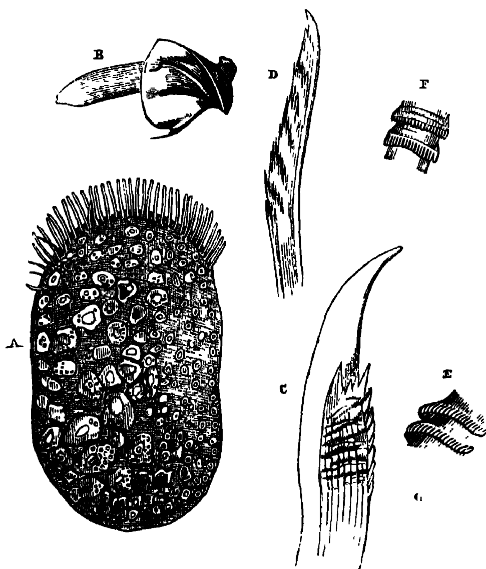


Fig. 52.—*Polynöe squamata*.
A, elytron viewed from above. B, a tooth. C, D, neuropodial setæ. E, F, parts of the blade of the same, more highly magnified. G, free extremity of a notopodial seta.

The apertures of the trichophores are placed between lobe-like prolongations of the neuropodium, to which the special term of *labia* (Grube) may be applied. In this species they present no remarkable peculiarity beyond their inequality.

The neuropodial setæ (Fig. 52, C, D), although at first sight very different from the notopodial setæ, are, in truth, constructed on essentially the same plan, the blade being short, while the handle is proportionally elongated. The blade is subcylindrical at its base, pointed and slightly curved. Eight or nine transverse ridges extend around about two-thirds of the circumference of its proximal half; the basal ridges are narrow, and merely serrated, but towards the apex the ridges become deeper, and the serrations pass into strong teeth; at the same time, one side of the ridge is elongated into a strong point.

Attached to the under surface of the parapodium by a somewhat enlarged base, with which it is articulated, is a smooth, conical, very flexible filament,—the *neuropodial cirrus* (Fig. 51, *c′*); it hardly reaches to the end of the neuropodium. Again, springing from the neural surface of the somite, close to the parapodium, there is a small pyriform tubercle (*h*), divided by longitudinal grooves into about eight segments. This is possibly connected with the reproductive function.

The appendage of the notopodium or rather of the notopodial side of the parapodium and somite, varies according to the particular somite which may be examined. In some somites this appendage is a cirrus (Fig. 51, D, *c*) similar to the neuropodial cirrus, but much larger, equalling the semidiameter of the body in length, and presenting an enlarged pigmented bulb of attachment to which the filament of the cirrus, which is cylindrical for about two-thirds of its length, and then becomes enlarged and suddenly tapers to its extremity, is articulated.

In the other somites the notopodial appendage is a large, thin, oval plate—the *elytron* (Fig. 51, C, *c*). It is attached by a thick peduncle, and has its long axis directed obliquely outwards and backwards. The surface of the elytron (Fig. 52, A) is covered with an ornamentation of larger or smaller tubercular prominences, granulated and ridged upon their surface. A part of the inner and anterior edge of each elytron overlaps or is overlapped by its fellows for

a certain extent of its circumference, which is so far smooth, but in the rest of its extent it is fringed with coarse brownish filaments or *fimbriæ*, which arise from the upper surface just within the edge, and are obviously outgrowths of the same order as the tubercles.

Such is the structure of one of the middle somites of *Polynöe squamata.* The anterior and posterior somites, with the exception of the first and second, present only minor differences, as in the proportions of the setæ, or in the figure of the elytra. The first somite, which contains the mouth, is the *peristomium* ("mund-segment" of Grube). The parapodia of this somite are narrow and elongated (Fig. 53, B, C, *m*); they are obscurely divided at their extremity into a rudimentary neuropodium and notopodium, and give attachment to a pair of large peristomial cirri (*c′ c*) ("cirrhes tentaculaires," Audouin and Milne-Edwards; "Fühler-cirren," Grube), of the same structure as the notopodial cirri, which stretch forwards by the sides of the mouth.

The apex of a single small aciculum issues rather above the point of division of the peristomial parapodium, and two minute curved setæ accompany it. These, have been generally overlooked; * but they seem to demonstrate, in a very interesting manner, the nature of the appendages of the peristomial segment.

The second somite differs from the rest only in the great elongation of its neuropodial cirrus, which is directed forwards and applied against the mouth.

The peristomium and the præstomium together are ordinarily confounded under the common term of "head." The latter (Fig. 53, B, C, *l*) is an oval segment flattened superiorly, placed altogether in front of and above the mouth, presenting on its postero-lateral edges four dark spots, the eyes, and possessing five cirriform appendages, two pairs and a single median one. The latter (*a*), or the *præstomial*

* At least, in the descriptions of the adult *Polynöe.* They are particularly mentioned, however, by Max Müller in his valuable paper, "Ueber die Entwickelung und Metamorphose der Polynoen." ('Müller's Archiv,' 1851.)

tentacle ("antenne médiane," Milne-Edwards) is similar in structure to an ordinary cirrus. Of the other appendages, the upper one upon each side (supero-lateral præstomial cirrus, "antenne mitoyenne") also resembles an ordinary cirrus (*b*); but the lower (infero-lateral præstomial cirrus, 'antenne externe") (*b'*) is much larger, and is capable of extreme elongation and contraction,* while the ordinary

Fig. 53.

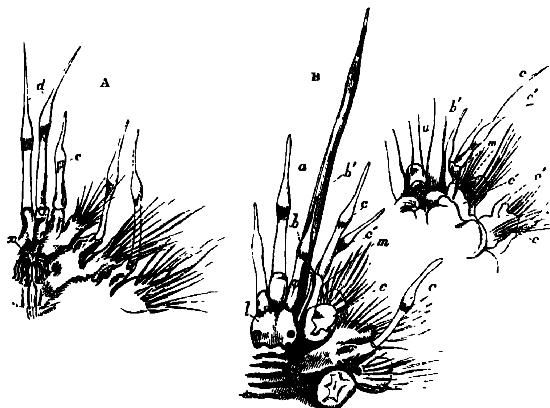


Fig. 53.—*Polynöe squamata.*
A. Posterior extremity from above: *c*, notopodial cirrus of last somite; *d*, pygidial cirri; *x*, anus.
B. Anterior extremity from above: *a*, præstomial tentacle; *b*, superior and *b'* inferior præstomial cirrus; *c*, *c'*, notopodial and neuropodial cirri; *e*, peduncle of first elytron: *l*, præstomium: *m*, parapodium of peristomium. C. Inferior view of anterior extremity, letters as before.

cirri are merely flexible. Although at first sight probable, yet it would appear from Max Müller's account of the development of *Polynöe,* that these two appendages do not, like the two peristomial cirri which they essentially resemble,

* I have never observed any invagination such as is stated to occur by Audouin and Milne-Edwards, 1834. ('Histoire Naturelle du Littoral de la France,' p. 10.)

correspond with the notopodial and neuropodial cirri of a single parapodium, inasmuch as they arise from perfectly distinct portions of the præstomium. It is very possible that each represents the appendage of a somite, and in this case the præstomium would be composed of at least two somites. Whether the præstomial tentacle indicates another, or whether it is merely an appendage of such a nature as the labrum or the rostrum of a Crustacean, there is no evidence at present to show.

It is highly interesting to remark, that thus, in the *Polynoe*, as in the *Arthropoda*, the "head" results from the modification of a number of somites, some of which lie in front of, and others behind, the mouth. The movements and evident extreme sensitiveness of the inferior præstomial cirri during life indicate that they perform the functions, as well as occupy the position, of antennæ.

The hindermost segment of the body, or *pygidium* (Fig. 51 B, Fig. 53 A), is narrow, and divided at the end into two supports for the pygidial (*d*) cirri, which are as long as the three last somites, and resemble the notopodial cirri in form and structure. They extend directly backwards, almost parallel with one another and with the notopodial cirri of the last somite, which are thrown backwards and downwards (Fig. 53, A, *c*). It seems probable that the pygidium represents only a single somite.

The anus is not terminal, as in many Annelids, but is seated in the middle of a strongly raised papilla (Fig. 53, A *x*), which projects from the dorsal surface of the penultimate somite; its sides are produced into about fourteen folds. The two last elytra have their edges excavated, so as to leave a space over the anus (Fig. 51, A *f*).

The notopodial cirri and the elytra do not coexist upon the same somites; and the order of arrangement of the elytrigerous and cirrigerous somites is very curious. The 1st or peristomial somite is cirrigerous, and so are the 3rd, 6th, 8th, 10th, 12th, 14th, 16th, 18th, 20th, 22nd, 24th, 25th, and 26th; while the 2nd, 4th, 5th, 7th, 9th, 11th, 13th,

15th, 17th, 19th, 21st, and 23rd somites bear elytra, making twelve pairs in all.

In no polychætous Annelid is the structure of a somite more complex than in *Polynöe*; and there are but very few parts not found in *Polynoe* to be met with in other *Annelida*. The careful study of this species, therefore, furnishes us with an almost complete nomenclature for the external organs of the whole group; and it will be found that the other forms of *Annelida* differ mainly in the greater or less development and modification of the organs which have just been described. A large proportion of the *Polychæta* are like *Polynöe*, free and actively locomotive animals, which rarely fabricate tubular habitations, and are therefore termed *Errantia*; they possess a præstomium, usually provided with eyes and feelers, and have many parapodia, which are not confined to the anterior region of the body. They very generally have a proboscis, provided with chitinous teeth.

The singular genus, *Tomopteris*, is a transparent pelagic Annelid, with numerous parapodia, each terminated by two lobes representing the neuropodium and notopodium, but with setæ, two of which are very long, only in the cephalic region.

The sedentary Annelids (*Tubicola*) fabricate tubes, either by gluing together particles of sand and shells, or by secreting a chitinous or calcified shelly substance, in which they remain (*e. g. Protula*, Fig. 54). The præstomium is small or wanting; none have a proboscis; there are no cirri; and the parapodia are short or rudimentary. The branchiæ are developed only on the anterior somites, and the latter are often markedly different from those which constitute the posterior part of the body.

In some (*Serpulidæ*) a tentacle is enlarged and its end secretes a shelly plate which serves as an operculum, and shuts down over the mouth of the calcareous tube inhabited by the animal, when it is retracted. The dilated end of the opercular tentacle sometimes serves as a chamber in which the young undergo their development, (species of *Spirorbis*).

The alimentary canal of the polychætous *Annelida* rarely

Fig. 54.

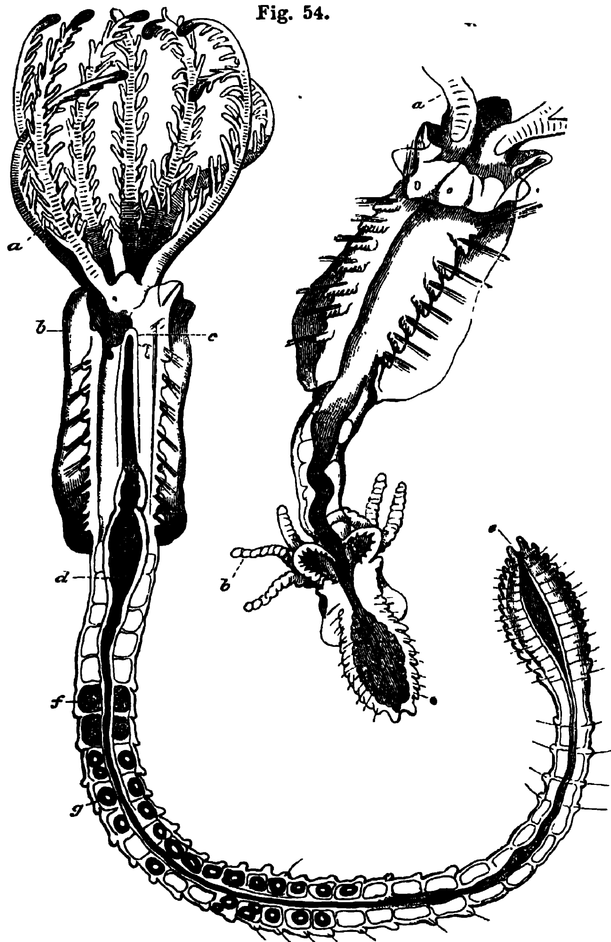


Fig. 54.—*Protula Dysteri.* A, the sexual, mature animal, extracted from its calcareous tube; *a*, branchial plumes; *b*, hood-like expansion of the anterior end of the body; *c*, the mouth; *d*, the stomach; *e*, the anus; *f*, the testes; *g*, the ova. B. a *Protula* in course of proliferation; *b*, the branchiæ of the zooid.

presents any marked distinction into stomach and intestine, and is almost always of the same length as the body, extending, without folds or convolutions, from its anterior to its posterior extremity; but in *Siphonostomum* (*Chlorœma*), *Pectinaria* and others, it is more or less convoluted. It is attached by membranous bands, or more complete mesenteries, to the walls of each somite, and very commonly presents a dilatation between every pair of mesenteries. In most *Polychæta*, the intestine acquires in this way merely a moniliform appearance, but in *Polynöe*, *Aphrodite*, *Sigalion*, and their allies, long cæca are given off upon each side of the alimentary canal, and, sometimes becoming more or less convoluted, terminate at the upper part of each segment (Fig. 51, D) close beneath, or in the branchiæ, where such organs exist.

The anterior portion of the alimentary canal is, in a great number of the *Polychæta*, in fact in all the typical *Errantia*, so modified as to constitute a distinct muscular pharynx, the anterior portion of the wall of which can be everted like the finger of a glove, from the aperture of the mouth, and the posterior portion protruded, so as to form a proboscis. In *Polynöe squamata*, the proboscis is one-fourth as long as the body, and its walls are very thick and muscular. At its anterior extremity it is surrounded with a circle of small papillæ, immediately behind which are four, strong, pointed and curved horny teeth, implanted in the muscular wall (Fig. 52, B). Each tooth has a little projection upon its convex edge, which is connected by a short strong ligament with the corresponding projection of another tooth; and the one pair of teeth, thus connected, works vertically against the opposite pair. In *Nereis*, there are two powerful teeth which work horizontally, besides minute accessory denticles. In *Syllis*, the chitinous lining of the pharynx is produced into a circle of sharp teeth anteriorly, and there is, in addition, a much stronger triangular median tooth. In *Glycera*, which possesses a pair of teeth, the extremity of the protruded proboscis is covered with very remarkable papillæ. The

most complex arrangement of teeth, however, is that presented by the *Eunicidæ*. In *Eunice*, there are altogether nine distinct pieces: two large, flat, more or less calcified portions united together below, and three cutting and tearing teeth on the right side working against four on the left. As has been already stated, the tubicolar Annelids possess neither proboscis nor teeth.

No special hepatic gland appears to exist in the *Annelida*, unless the intestinal cæca perform that function, and the secretion of the bile is doubtless effected by the glandular tract, which extends for a greater or less distance in the walls of the alimentary canal. A pair of glandular cæca, the function of which is not known, is appended to the base of the proboscis in *Nereis*.

The general cavity of the body, or perivisceral cavity, which is included between the parietes of the alimentary canal and those of the body, is filled with a fluid which contains corpuscles, which are usually, as in the *Invertebrata* in general, colourless. They are red, however, in *Glycera*, and in a species of *Apneumea* (De Quatrefages). The parapodia, the cirri, the branchiæ, and all the other important appendages of the *Polychæta* contain a cavity continuous with the perivisceral cavity, and are therefore equally filled with the blood. The circulation of this fluid is effected partly by the contraction of the body and its appendages, partly by the vibratile cilia, with which a greater or less extent of the walls of the perivisceral cavity is covered.

In a great number of the *Polychæta* no part of the body is specially adapted to perform the function of respiration, the aeration of the blood probably taking place wherever the integument is sufficiently thin; and, even when distinct branchiæ ordinarily exist, members of the same family may be deprived of them. In *Polynöe squamata*, ciliated spots which appear to represent branchiæ, may be discovered on the dorsal side of the bases of the parapodia, at any rate, in young specimens. In some species of *Polynöe* the parapodia give rise, at corresponding points, to large, richly ciliated, malleiform tubercles, in which the cæca of

the alimentary canal terminate. In *Sigalion*, a filiform, ciliated branchia depends from the upper part of the somite, beneath the elytron; and besides this, curious little ciliated palettes are arranged upon the dorsal surface of the parapodia, and upon the sides of the anterior somites. But the best developed branchiæ among these Annelids are possessed by the *Amphinomidæ*, and the *Eunicidæ* among the *Errantia*; the *Terebellidæ*, and the *Serpulidæ* among the *Tubicola*. In the three former families the branchiæ are ciliated branched plumes, or tufts, attached to the dorsal surface of more or fewer of the somites. In the last (Fig. 54) they are exclusively attached to the anterior segment of the body, and present the form of two large plumes, each consisting of a principal stem, with many lateral branches. The stem is supported by a kind of internal skeleton, of cartilaginous consistence, which sends off processes into the lateral branches.

I have been unable to find any pseud-hæmal vessels in *Polynöe squamata*, and as Claparède * could discover none in the transparent *P. lunulata*, it is safe to assume their nonexistence. Claparède, in fact, denies them to the whole of the *Aphroditidæ*.

When it is present, the pseud-hæmal system varies very much in the arrangement of its great trunks; but they commonly consist of one or two principal longitudinal dorsal and ventral vessels, which are connected in each somite by transverse branches. Where branchiæ exist, loops or processes of one or other of the great trunks enter them. The dorsal and the ventral trunks are usually rhythmically contractile, and contractile dilatations at the bases of the branchiæ (*Eunice*), in portions of the lateral trunks (*Arenicola*), or in those which supply the proboscis (*Eunice, Nereis*), have received the name of "hearts." The direction of the contractions is usually such that the blood is propelled from behind forwards in the dorsal vessel, and in the opposite direction in the ventral vessel; but the course which it pursues in the lateral trunks

* 'Annélides Chétopodes du Golfe de Naples,' 1868, p. 65.

is probably very irregular. In *Chlorœma*, in which even the smallest ramifications of the vessels are contractile, I have observed cæcal branches depending into the perivisceral cavity in which the contained fluid underwent merely an alternate flux and reflux. Ramified cæca of a similar kind appear to exist in the oligochætous genera, *Euaxes* and *Lumbriculus*. The principal trunks give off a great number of branches, which ramify very minutely in some Annelids (*Eunice*) and may give rise to retia mirabilia (*Nereis*); but in many (*e.g. Protula*), there are hardly any branches and no minute capillary ramifications.

In many *Polychæta* no segmental organs have yet been discovered, and in others they appear to be represented by mere openings in the parietes of the body. I have observed short ciliated canals opening externally upon the ventral surface at the bases of the parapodia in *Phyllodoce viridis*, and there are indications of the existence of similar organs in *Syllis vittata*. True segmental organs have, however, been found by Ehlers and Claparède in many *Polychæta*. In some cases their walls are thick and glandular, and they probably have a renal function. In addition, they frequently play the part of oviducts and spermiducts. Whether the ciliated canal extending along the ventral surface of the intestine, which I have described in *Protula*, is a structure of the same order or not, I am not prepared to say.

The nervous system of the *Polychæta* usually consists of a chain of ganglia,—one pair for each somite,—connected together by longitudinal and transverse commissural bands, which diverge between the cerebral ganglia and the succeeding pair, to allow of the passage of the œsophagus. The most important differences presented by the nervous systems of the *Polychæta*, result from the varying length of the transverse commissures. In *Vermilia, Serpula, Sabella*, these commissures are very long, so that two distinct and distant series of ganglia appear to run through the body, while, in *Nepthys*, the two series of ganglia are fused into a single cord enlarged at intervals. Every transitional

condition between these is observable in *Terebella*, *Aonia*, *Glycera*, *Phyllodoce*, and *Aphrodite*. In most *Polychæta* a very extensive series of visceral nerves supplies the alimentary canal.

The recognisable organs of sense in the *Annelida* are eyes and auditory vesicles. The former are usually very simple, consisting of an expansion of the extremity of the optic

Fig. 55.

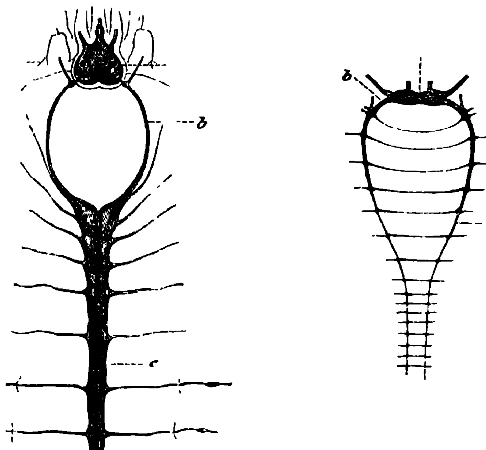


Fig. 55.—A. Anterior end of the nervous system of *Polynoe squamata* (after De Quatrefages): *a*, cerebral ganglia; *b*, œsophageal commissures; *c*, longitudinal commissures of the ventral ganglia.
B. Anterior end of the nervous system of *Sabella flabellata* (after De Quatrefages): *a*, cerebral ganglia; *b*, œsophageal commissures; *c*. longitudinal commissures of the ventral ganglia. Those of opposite sides are united by long transverse commissures.

nerve, imbedded in pigment, and provided occasionally, but not invariably, with transparent spheroids or cones. *Alciope* and *Torrea* have very well developed and large eyes. The eyes are usually confined to the anterior extremity of the body, and to the præstomium where it exists; but, in the remarkable genus *Polyophthalmus*, De Quatrefages discovered,

besides the ordinary cephalic eyes, a double series of additional visual organs, one pair being allotted to each somite. In *Branchiomma*, eyes are situated at the ends of the branchial plumes. Ehrenberg has described two caudal eyes in *Amphicora*, and De Quatrefages has shown that similarly placed eyes exist in three other species of *Polychæta*, two of which are closely allied to *Amphicora*, while the other is an errant form, related to *Lumbrinereis*. These curious worms are said to swim about with the caudal extremity forwards.

Auditory sacs, containing many otoliths, have been observed upon each side of the œsophageal ring in *Arenicola*, and similar organs have been noticed in other *Tubicola*; but hitherto their existence has not been certainly determined in the *Errantia*.

The genitalia of the polychætous *Annelida* are excessively simple in their structure; indeed, special reproductive organs can hardly be said to exist in most, the generative products being merely developed from some part of the walls of the perivisceral cavity, in which they eventually freely float, making their way out in a manner which is not quite understood at present; probably, however, through temporary or permanent apertures at the bases of the parapodia. In many, the segmental organs appear to serve as excretory ducts. As a rule, the polychætous Annelids are diœcious; but some (*e.g. Protula*, Fig. 54) are hermaphrodite. The ova undergo their development within the body of the parent in some species of *Eunice*; in pouches attached to the body in *Exogone*; in masses of gelatinous matter which adhere to the tubes of the vermidom in *Protula*; beneath the elytra in *Polynöe cirrata*; in the cavity of the opercular tentacle in some *Spirorbes*; while, in other cases, they appear to become, almost immediately, free ciliated embryos.

The vitellus undergoes division, and is converted, as in the case of the *Oligochæta* and *Hirudinea*, into blastomeres of two kinds. This contrast between the two components of the embryo commences with the division of the vitellus into

two, inasmuch as the first fissure is usually so directed as to divide the yelk into unequal portions. Both subdivide, but the smaller much faster than the larger; so that the former becomes converted into very small blastomeres, which gradually envelope the larger blastomeres resulting from the subdivision of the latter. The larger included blastomeres are destined to form the alimentary tract; the smaller peripheral ones, on the other hand, give rise to the ectoderm, and to the nervous ganglia.* As in the *Oligochæta* and *Hirudinea*, again, the mesoblast forms a thick band on each side of the median ventral line, and its transverse division originates the segmentation of the body. But, generally, the development of the *protosomites*, as these segments might be called, does not occur until some time after the embryo has been hatched. The somites increase in number by the addition of new ones between the last and the penultimate somite.

The embryos of the *Polychæta* differ from those of the *Oligochæta* and *Hirudinea* in being ciliated. In some cases, the cilia form a broad zone which encircles the body, leaving at each end an area, which is either devoid of cilia, or, as is frequently the case, has a tuft of long cilia at the cephalic end. Such larvæ are termed *Atrocha*.

In other embryos the cilia are arranged in one or more narrow bands, which surround the body. A very common arrangement is one in which a band of cilia encircles the body immediately in front of the mouth, the region in front of the band bearing eyes, and becoming the præstomium of the adult (*e.g. Polynöe*). In such embryos, there is very commonly a second band of cilia around the anal end of the embryo, and a tuft of cilia is attached to the centre of the præstomium. These larvæ are called *Telotrocha*. In other cases, one or many bands of cilia surround the middle of the body, between the mouth and the hinder extremity. These are *Mesotrocha*.

In the telotrochous larva of *Phyllodoce* a shield-shaped,

* Claparède and Metschnikoff, 'Beiträge zur Kenntniss der Entwickelungsgeschichte der Chaetopoden,' 1868.

mantle-like, elevation of the integument covers the dorsal region of the body behind the præ-oral ciliated ring. In the larvæ of the *Serpulidæ* a process of the integument grows out behind the mouth, and surrounds the anterior part of the body of the larva like a turned-back collar. It persists, as a kind of hood, in the adult.

Some larvæ are provided with setæ of a different character from those which are possessed by the adult, and which are cast off as development advances.

Many *Polychæta* multiply by a process of zooid development, which, in some cases, appears to be a combination of fission with gemmation; in others, to approach very nearly to pure fission or pure gemmation. The result is, not infrequently, the formation of long chains of connected zooids.

The method of multiplication which De Quatrefages observed in *Syllis prolifera*, is nearly simple fission, the animal dividing near its middle, and the posterior division acquiring a new head.

In *Myrianida*, Milne-Edwards has described the occurrence of a sort of continuous budding between the ultimate and penultimate segments, in which region new segments are formed until the zooid has attained its full length.

Frey and Leuckart and Krohn have shown that *Autolytus prolifer* multiplies in a somewhat similar manner; but, instead of each new zooid being formed at the expense of an entire somite, it is developed from only a portion of one. Finally, I found in *Protula Dysteri* that, when the *Protula* had attained a certain length, all the somites behind the sixteenth became eventually separated as a new zooid; but the development of the latter is not mere fission, inasmuch as one of the earliest steps in the process is the enlargement of the seventeenth somite, and its conversion into the head and thorax of the bud (Fig. 54, B). Sars has described a similar mode of multiplication in his *Filograna implexa*, a very closely allied form.

In *Syllis* and in *Protula*, the producing and the produced zooids alike develope generative products, but in *Autolytus*,

Krohn has shown that the primary producing zooid remains sexless, the secondary produced zooids having a somewhat different form, and alone giving rise to ova and spermatozoa.

In some species of the genus *Nereis*, the worm, after the development of its genital organs has taken place, takes on the characters of what was formerly considered a distinct genus, *Heteronereis*; and the males and the females of the same species of *Nereis* have even been regarded as different species of *Heteronereis*.*

The series of forms represented by the *Turbellaria*, the *Hirudinea*, the *Oligochæta*, and the *Polychæta*, illustrates the manner in which a type of organisation, which, in its simplest condition, exhibits but little advance upon a mere Gastrula, passes into one in which the body is divided into many segments, each provided with a pair of appendages or rudimentary limbs.

The segmentation, or serial repetition of homologous somites, extends to the nervous system, and, more or less, to the vascular and reproductive organs, in the higher forms of these "Annulose" animals; from which a further extension of the same process of segmentation, with a fuller development of the appendages and a more complete appropriation of some of them to manducatory purposes, leads us to the *Arthropoda*.

The GEPHYREA.—These are marine vermiform animals without distinct external segmentation or parapodial appendages. The ectoderm has a chitinous cuticle, and is often provided with tubercles, hooks, or setæ of chitin (*Echiurus*, *Sternaspis*). No calcareous skeleton is found in any of the *Gephyrea*. The integument frequently contains numerous simple glands, the apertures of which perforate the cuticle. In one genus (*Sternaspis*), two shield-shaped plates, fringed with setæ, are developed upon the hinder part of the

* Ehlers, "Die Gattung *Heteronereis*." ('Göttingen Nachrichten,' 1867.)

ventral surface of the body. There are external circular, and internal longitudinal muscular fibres beneath the ectoderm. An inner layer of circularly disposed muscular fibres may be added. The oral end of the body may have the form of a retractile proboscis (*Priapulus*), or be provided with tentacular appendages. These may be arranged in a circle round the mouth, and short (*Sipunculus*, Fig. 56, I. T), or long (*Phoronis*), or there may be a single long, sometimes bifurcated and ciliated, tentacular appendage (*Bonellia*). Filamentous appendages, which are probably branchiæ, are given off at the hinder end of the body in *Sternaspis* and *Priapulus*. The endoderm is usually ciliated throughout. The intestine is straight in most genera, but is coiled and bent upon itself, so as to terminate in the middle of the body, in *Sipunculus* (Fig. 56, I.). In *Phoronis* the anus is close to the mouth. The anal aperture is always situated upon the dorsal aspect of the body. There is a spacious perivisceral cavity undivided by mesenteries, which in some cases (*Priapulus*, *Sipunculus*) opens externally by a terminal pore. In *Echiurus*, *Bonellia*, *Thalassema*, a pair of tubular, sometimes branched organs, which are ciliated internally, and communicate by ciliated apertures with the perivisceral cavity, open into the rectum. These appear to represent the water-vessels of the *Rotifera* and the respiratory tubes of the *Holothuriæ*.

A pseud-hæmal system exists in most (*Sipunculus*, *Sternaspis*, *Bonellia*, *Echiurus*, and *Phoronis*), and, when fully developed, consists of two longitudinal trunks—one dorsal, or supra-intestinal, the other ventral, with their terminal and lateral communications. The pseud-hæmal fluid is colourless, or may have a pale reddish tinge, in most. In *Phoronis* it is said to contain red corpuscles. In *Sipunculus*, the cavities of the tentacles communicate with a circular vessel provided with cæcal appendages; and this circular vessel is said to open into the pseud-hæmal vessels.

The nervous system presents a collar, which surrounds the œsophagus, and from which a simple or ganglionated

cord proceeds backwards in the ventral median line.

Fig. 56.

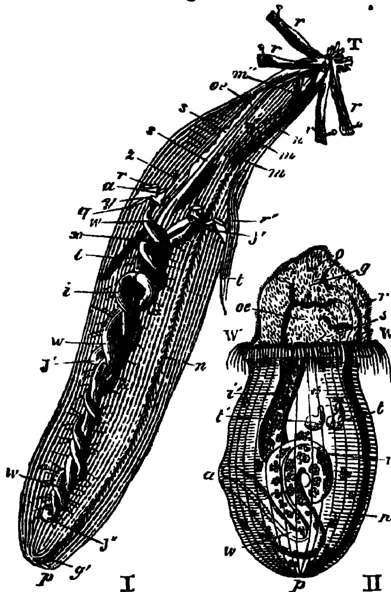


Fig. 56.—*Sipunculus nudus* (after Keferstein and Ehlers) *

1. The animal laid open longitudinally—⅓ n.s. T; tentacles; *r*, the four retractor muscles of the proboscis; *r*, the points at which they were attached to the walls of the body; *œ*, œsophagus; *i*, intestine; *a*, anus; J, J′, loops of the intestine; *x*, *y*, appendages of the rectum; *z*, fusiform muscle; *w*, ciliated groove on the inner side of the intestine; *q*, anal muscles; *s*, cæcal glands; *t*, cæca which open on each side of the nervous cord, and are generally considered to be testes; *p*, pore at the hinder end of the body; *n*, nervous cord, which ends in a lobed ganglionic mass, close to the mouth, and presents an enlargement, *g*′, at its posterior end; *m*, *m*′, *m*″, muscles associated with the nervous cords.

II. A larval Sipunculus about $\frac{1}{12}$ of an inch long.—*o*, mouth; *œ*, gullet; *s*, cæcal gland; *i*, intestine with masses of fatty cells; *a*, anus; *w*, ciliated groove of the intestine; *g*, brain with two pairs of red eye-spots; *n*, nervous cord, *p*, pore; *t*, *t*, so-called testes; W W, circlet of cilia.

giving off lateral branches. The ventral cord contains a

* 'Zoologische Beiträge,' 1861.

central canal, and the collar usually presents a cerebral ganglionic enlargement. Rudimentary eyes are sometimes connected with the cerebral ganglion.

The sexes are distinct, and the reproductive elements are developed either from the parietes of the perivisceral cavity or in simple cæcal glands. In *Sipunculus*, the ova and spermatozoa float freely in the perivisceral cavity.

The actively locomotive embryo of *Sipunculus* (Fig. 56, II) is surrounded by a circular band of cilia placed immediately behind the mouth (w, w), and resembles a Rotifer or a mesotrochal Annelidan larva. As development advances it loses this apparatus, and passes gradually into the adult form. In *Phoronis*, the embryo is also mesotrochal, but it has two ciliated bands, one circular, round the anus, and the other immediately behind the mouth. The post-oral band of cilia is produced into numerous tentaculiform lobes, and fringes the free edge of a broad concave lobe of the dorsal side of the body, which arches over the mouth. In this state the embryo is the so-called *Actinotrocha*.* An invagination of the ventral integument of the larva connects itself with the middle of the intestine, and then, becoming evaginated, pulls the intestine, in the form of a loop, into the ventral process thus formed, which gives rise to the body of the *Phoronis*, while the tentacles of the larva grow into those of the adult. Schneider has suggested that the bell-shaped larva, with long setæ, termed *Mitraria* by Müller, is the embryo of *Sternaspis*.

The affinities of the *Gephyrea* with the *Turbellaria*, with the *Annelida*, and with the *Rotifera*, are unmistakable. In fact, it may be doubted whether *Sternaspis* should not be associated with the *Polychæta*, and *Bonellia* is in many respects comparable to a colossal Rotifer. Their usually assumed connexion with the *Echinodermata* is more questionable. The circular canal which communicates with the cavities of the tentacles in *Sipunculus* has been compared to the ambulacral system of the Echinoderms, but the

* Schneider. "Ueber die Metamorphose der *Actinotrocha branchiata*." ('Archiv für Anat.,' 1862.)

manner of its development is not yet sufficiently understood to justify the expression of an opinion on this subject. Krohn has described a bilobed organ on the ventral face of the gullet of the larva of Sipunculus, which opens externally in front of the ciliated band by a narrow ciliated duct * (Fig. 56, II. s). It has a striking similarity to the "water-vessel" of the larva of *Balanoglossus*, which, however, lies on the opposite side of the body.

* "Ueber die Larve des *Sipunculus nudus.*" ('Archiv für Anat.,' 1851)

CHAPTER VI.

THE ARTHROPODA.

The segmentation of the body, that is, its division into a series of somites, each provided with a pair of lateral appendages, which is so characteristic a feature of the higher Annelids, is exhibited in a still more marked degree by the *Arthropoda*. In these animals, moreover, the appendages themselves are usually divided into segments, while one or more pairs of the appendages in the neighbourhood of the mouth are modified in form and position to subserve manducation. Segmental organs, at least in their Annelidan form, are wanting in the *Arthropoda*, and neither in the embryonic nor the adult condition do they ever possess cilia.

The process of yelk-division may be complete or incomplete, but no known Arthropod ovum gives rise to a vesicular morula, nor is the alimentary cavity ordinarily formed by invagination.* The precise mode of origin of the mesoblast has yet to be worked out, but the perivisceral cavity appears always to be developed by its splitting. In other words it is a *schizocœle*.

As with Annelids, the segmentation of the body results from the subdivision of the mesoblast by transverse constrictions into *protosomites*; and there is every reason to believe that the ganglionated nervous chain arises from an involution of the epiblast.

* The recent observations of Bobretzky on the development of *Oniscus* and *Astacus* (Hofmann and Schwalbe, 'Jahresberichte,' Bd. ii., 1875) however tend to show that the hypoblast arises by a sort of modified invagination of the primitive blastoderm. And in other *Arthropoda* there are indications of a similar process.

The neural face of the embryo is fashioned first, and its anterior end terminates in two rounded expansions—the *procephalic* lobes—which are converted into the sides and front of the head. The appendages are developed as paired outgrowths from the neural aspect of each somite, and whatever their ultimate form, they are, at first, simple bud-like processes. Very generally, a broad median prolongation of the sternum of the somite which lies in front of the mouth, gives rise to a *labrum*; while a corresponding, but often bifid median elevation, behind the mouth, becomes a *metastoma.*

In many Arthropods, the hæmal or tergal face of the body grows out into lateral processes, which may either be fixed, or more or less moveable. The lateral prolongations of the carapace in the *Crustacea* and the wings of *Insecta* are structures of this order.

In a number of Insects belonging to different orders of the class, an amnionic investment is developed from the extra-neural part of the blastoderm by a method similar to that which gives rise to the amnion in the higher *Vertebrata.*

In all the higher Arthropods, a certain number of the somites which constitute the anterior end of the body coalesce and form a *head,* distinct from the rest of the body; and the appendages belonging to these confluent somites undergo remarkable modifications, whereby they are converted into organs of the higher senses and into jaws. In many cases, the somites of the middle and posterior parts of the body become similarly differentiated into groups of polysomitic segments, which then receive the name of *thorax* and *abdomen.* The somites entering into each of these groups may remain distinct or may coalesce. The tergal expansions of the somites of the head, or of both head and thorax, may take the shape of a broad shield, or *carapace.* This may constitute a continuous whole (*e.g. Apus, Astacus*); or its two halves may be moveably connected by a median hinge, like a bivalve shell (*Cypris, Limnadia*); or finally, the tergal processes of each side may remain dis-

tinct from one another and freely moveable on their respective somites (wings of Insects).

Limbs, or appendages capable of effecting locomotion, are always attached either to the head or to the thorax,* or to both. They may be present or absent in the abdominal region. In adult *Arachnida* and *Insecta*, there are no abdominal limbs, unless the accessory organs of generation, the stings of some insects, and the peculiar appendages of the abdomen in the *Thysanura* and *Collembola* be such.

The alimentary apparatus presents very wide diversities in form and structure, and in the number and nature of its glands. The anus, which is very rarely absent, is situated in the hindermost somite.

In like manner, the blood-vascular system varies from a mere perivisceral cavity without any heart (*Ostracoda, Cirripedia*) up to a complete, usually many-chambered heart with well-developed arterial vessels. The venous channels, however, always have the nature of more or less definite lacunæ. The blood corpuscles are colourless, nucleated cells.

Special respiratory organs may be absent, or they may take one of the following forms.

1. *Branchiæ.* Externally projecting processes of the body or limbs, supplied with venous blood, which is thus brought into contact with the air dissolved in water.

2. *Tracheæ.* Tubes which traverse the body and generally open upon its exterior by apertures termed *stigmata*, and thus bring air into contact with the blood and the tissues generally. Saccular reservoirs of air are often formed by dilatations of these tubes.

The so-called *Tracheo-branchiæ* of some aquatic Insect larvæ are usually laterally projecting processes of more or fewer of the thoracic or abdominal somites, containing abundant tracheæ, which communicate with those which traverse the body (*Ephemeridæ, Perlaridæ*). They are in no sense branchiæ, but simply take the place of stigmata. The exchange of constituents between the air contained

* The extinct *Trilobites* possibly form an exception to this rule.

in the tracheæ of these animals and that of the surrounding medium, is effected indirectly, by diffusion through the walls of the tracheo-branchiæ, instead of directly, through the stigmata, as in other cases.

In the aquatic larvæ of many Dragon-flies (*Libellulidæ*), the function of the tracheo-branchiæ is performed by folds of the lining membrane of the rectum, which contain abundant tracheæ. Water is drawn into, and expelled from, the cavity of the rectum by rhythmical contractions of its walls, so as to secure the exchange of gaseous constituents between the air which it contains and that which fills the tracheæ.

3. *Pulmonary sacs.* These are met with only in some *Arachnida.* They are involutions of the integument, the walls of which are folded in such a manner as to expose a large surface to the air, which is alternately taken into, and expelled from, their apertures. The blood is brought to these sacs by venous channels.

The exact mode by which the separation of the nitrogenous products of the waste of the tissues from the blood is effected in Arthropods requires further elucidation. In many however, such products, notably uric acid, have been found to abound in the *corpus adiposum*—a cellular mass which lies in the walls of, and more or less fills, the perivisceral cavity—and in the Malpighian glands. In the latter case, they are conveyed out of the body by the intestine.

The nervous system consists primitively of a pair of ganglia for each somite, but the number of ganglia discoverable in the adult depends on the extent to which these primitive ganglia coalesce. There is usually, if not always, a well-developed system of ganglionated visceral nerves, connected with the cerebral ganglia and distributed to the gullet and stomach.

Eyes are usually present; and, when they exist, they are almost always situated in the head and are connected with the cerebral ganglia. Among the *Crustacea*, however, *Euphausia* has eyes in some of the thoracic limbs, and in some abdominal somites. The eyes may be simple or compound.

In the latter case there are, in correspondence with the number of parts into which the transparent corneal continuation of the chitinous cuticula over the eye is divided, a number of elongated bodies which lie between the outer surface of the ganglionic expansion of the optic nerve and the inner face of the cornea. These bodies consist of two parts: an external transparent *crystalline cone* and an internal *prismatic rod.* The broad end of the cone is external, and is applied to the inner surface of the corneal facet; its narrow end is continuous with the outer extremity of the prismatic rod, which, by its inner end, is connected with the ultimate ramifications of the optic nerve. Each of these crystalline cones and prismatic rods is separated from the rest by a pigmented sheath.*

Distinct auditory organs have been observed in Crustaceans and Insects. They are not exclusively confined to the head. In the opossum shrimp (*Mysis*), for example, they are placed in the appendages of the last somite of the abdomen. And in Insects, the only organs to which the auditory function can be certainly assigned are situated in the thorax or in the legs.

There is some reason to think that the antennæ of Insects are the seat of the olfactory function, but no certain information on this head has been obtained. The very fine setæ to the bases of which nerves can be traced, which abound on the antennary organs of *Insecta* and *Crustacea*, but are found in other regions of the body, are probably partly tactile and partly auditory organs.

As a general rule, all the muscles of the *Arthropoda*, even those of the alimentary canal, are striated. Those of the body and limbs are often attached by chitinised tendons to the parts which they have to move. As the hard skeleton is hollow and the muscles are inside it, it follows that the body, or a limb, is bent towards that side of its axis, which

* Leydig, 'Das Auge der Gliederthiere,' 1864 Schulze, 'Untersuchungen,' 1868. Mr. E. T. Newton has given a very good account of the structure of the eye of the lobster, accompanied by full references to the literature of the subject, in the 'Quarterly Journal of Microscopical Science' for 1875.

is opposite to that on which a contracting muscle is situated.

Sounds are produced by many Insects; but in most cases, they cannot be properly referred to a voice, in the sense in which that term is applied to the sounds produced in the higher animals, by the vibrations of the atmosphere arising from the impact of a current of air upon the free edges of membranes bounding the aperture of exit of the current. The chirping and humming of Insects often arise from the friction of their hard parts against one another, or from the rapid vibration of their wings: in some instances, however, recent investigations render it probable that they are produced by the action of expiratory currents on tense membranes which bound the stigmata.

Agamogenesis is very common among some groups of the *Arthropoda*, such as the *Crustacea* and the *Insecta*. but has not yet been observed in the *Myriapoda* or the *Arachnida*. It may be effected in one of two ways:

1. Either individuals which are, by their structure, incapable of being impregnated and are therefore physiologically sexless, though it may happen that they more or less approximate females morphologically, give rise to offspring (*Cecidomyia* larvæ, *Aphis*);

2. Or individuals which are capable of being impregnated, and are thus both morphologically and physiologically true females, give rise to eggs which develope without impregnation. (The queen bee, so far as the production of drones is concerned; many *Lepidoptera*.)

The cases of *Apus*, *Daphnia* and *Cypris* would belong to the latter category, if it were certain that the very same females which, for a certain period, produce young agamogenetically, at another time undergo fecundation. Multiplication by fission or external gemmation is not known to take place in any Arthropod. Hermaphrodism occurs as a rule in some few Arthropods (*e.g.* the *Cirripedia* and *Tardigrada*), and as an abnormal 'sport' in sundry *Crustacea* and in many *Insecta*.

In absolute number of species, the *Arthropoda* far exceed all the rest of the animal kingdom put together. Thus Gerstaecker,* while allowing 50,000 species for the latter, estimates the number of species of *Arthropoda* as rather above than below 200,000; by far the larger proportion of these, probably more than 150,000, being Insects.

The *Arthropoda* are commonly divided into the *Crustacea*, the *Arachnida*, the *Myriapoda*, and the *Insecta*; and though it is impracticable to give a definition which shall absolutely separate the first two groups, it is perhaps not worth while to disturb an arrangement which has much practical convenience. But, for purely morphological purposes, it may be instructive to regard them from another point of view.

The *Arthropoda* may, in fact, be divided into two series. One of these consists almost wholly of air-breathing forms, which, if they possess special respiratory organs, have either pulmonary sacs or tracheæ, or both combined; while the other includes a corresponding predominance of water-breathing animals, which, if they possess respiratory organs, have branchiæ. The latter series contains the *Crustacea*; the former comprises the *Arachnida*, *Myriapoda*, and *Insecta*.

In the course of the development of the higher *Arthropoda*, there is a stage in which the body begins to be segmented, but the appendages are not developed. This is followed by a stage in which appendages make their appearance, but the antennary and manducatory appendages (*gnathites*) are like the other limbs: and, finally, there is a stage in which the gnathites are completely converted into jaws. Now, among the water-breathing *Arthropoda*, no trace of limbs has yet been certainly discovered among the *Trilobita*; in the *Merostomata* (*Eurypterida* and *Xiphosura*) the gnathites are completely pediform; while, in the *Entomostraca* and *Malacostraca*, more or fewer of the gnathites are so modified as to subserve manducation and no other function.

* Bronn's 'Klassen und Ordnungen des Thierreichs,' vol. v. p. 273. 1868.

In the air-breathing series, no completely apodal forms are known. The *Tardigrada* and the *Pentastomida* appear to have no jaws; but the presence of oral stilets in the former, and the position of the hooks which represent the limbs in the latter, throw some doubt upon this point.

In the *Arachnida* and the *Peripatidea* the gnathites are completely pediform. But, in the *Myriapoda*, and still more in the *Insecta*, the gnathites lose the character of legs, and are completely converted into manducatory organs. Thus we arrive at the following arrangement of the *Arthropoda*:—

ARTHROPODA.

I. Without Gnathites.

TRILOBITA. TARDIGRADA (?) PENTASTOMIDA (?)

II. With Pediform Gnathites.

MEROSTOMATA. ARACHNIDA. PERIPATIDEA.

III. With Maxilliform Gnathites.

ENTOMOSTRACA.	MYRIAPODA.
MALACOSTRACA.	INSECTA.
Water-breathers.	Air-breathers.

For the most part.

Of the four great groups, the *Crustacea* are those which present the greatest and the most instructive variations upon the fundamental type of structure; while the modifications of the *Insecta*, *Arachnida*, and *Myriapoda*, are less extensive, and may be regarded as of secondary morphological importance. The *Crustacea* will therefore be treated of at some length, while the other groups will be passed over more lightly.

THE CRUSTACEA.

The TRILOBITA.—These ancient Arthropods, which have been extinct since the latter part of the Palæozoic epoch, occur in the fossil state in great numbers, and in conditions very favourable for their preservation; but, up to this time, no certain indications of the existence of appendages, nor even of any hard sternal body-wall, have been discovered, though a shield-shaped labrum, which lies in front of the mouth, has been preserved in some specimens. The body consists of a *cephalic shield* (Fig. 57, A); of a variable number of movably articulated *thoracic somites* (Fig. 57, B); and of a *pygidium*, composed of a variable number of the somites which succeed the thorax, united together (Fig. 57, C).

Each thoracic somite presents a median portion, convex from side to side, termed the *axis* or *tergum*, and two flattened lateral portions, the *pleura*. The former overlap one another largely when the body is extended; the latter, when it is flexed; and the freedom of motion permitted by this arrangement is so great, that many Trilobites were able to roll themselves up like woodlice, and are found fossilised in that condition. At the lateral edge of each pleuron, the cuticular substance of which it is composed folds inwards, and can be traced on the ventral or sternal side for some distance. But in the middle of the ventral region no indication of a sternum is discoverable. It may therefore be concluded that the sternal region of the somite was of a soft and perishable nature; and that the thoracic somite of a Trilobite resembled one of the abdominal somites of a crab in this and in some other respects.

The *glabellum* (Fig. 57, 4), or central raised ridge of the cephalic shield, is a continuation of the thoracic *axis*, the lobation of its sides perhaps referring to the number of primitive somites it represents. The *limb*, or lateral area on either side, answers to a thoracic *pleuron*; its thickened margin (Fig. 57, 1) is produced into two longer

or shorter posterior angles (*g*); inferiorly, the marginal band is reflected inwards for a short distance, as the *subfrontal fold*, the remaining sternal area being incomplete. A median moveable plate answers to the labrum of *Apus* and *Limulus*. On the occipital or lateral margin of the

Fig. 57.

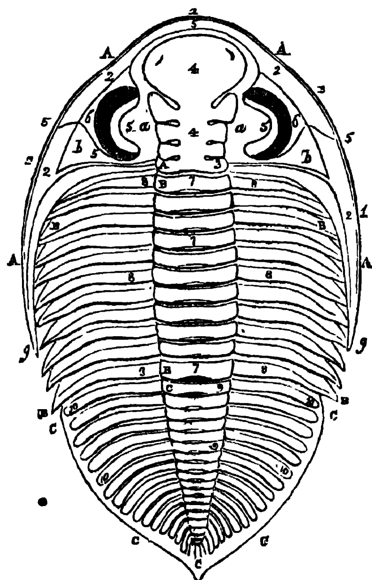


Fig. 57.—Diagram of *Dalmanites* (after Pictet).—A, head; 1, marginal band; 2, marginal groove, internal to the band; 3, occipital segment; 4, glabellum; 5, great suture; 6, eyes; *a*, fixed gena; *b*, separable gena; *g*, genal angle; B, thorax; 7, axis or tergum; 8, pleuron; C, pygidium; 9, tergal; 10, pleural portions of the pygidium.

limb a suture (Fig. 57, 5) commences, and passing between the eye and the glabellum, meets that of the opposite side either in front of the latter, or on the margin of the limb, or on the subfrontal fold, and is connected with the labral

suture by one or two sutures. The limb is thus divided into two parts—one fixed (the *fixed gena*, Fig. 57, *a*), attached to the glabellum; the other separable (the moveable *gena*, Fig. 57, *b*), on which the eye is placed. The eyes are absent in some genera. In others, they occur as isolated ocelli; or in groups, their interspaces being occupied by the common integument; or they may resemble the compound eyes of other *Arthropods*.

M. Barrande* has succeeded in tracing out the development of some species of Trilobites. He finds that the smallest, and therefore youngest, forms are discoidal bodies, without any clear evidence of segmentation. The division into somites takes place by degrees, the number increasing up to the adult condition. It is possible that still younger conditions may have escaped fossilisation, but the analogy of *Limulus* suggests that these small discoidal forms really represent the condition in which the Trilobite left the egg.

The MEROSTOMATA.†—The only existing representative of this division of the *Crustacea* is the genus *Limulus* (the King Crabs or Horse-shoe Crabs), the various species of which are found in America and in the Moluccas. They are usually classed as a distinct order of the *Crustacea*, termed *Xiphosura* or *Pœcilopoda*.

The body of Limulus (Fig. 58) is naturally divided into three parts, which are moveably articulated together. The most anterior is a shield-shaped portion, curiously similar in form to the head of a Trilobite. Its convex dorsal surface is similarly divided into a median and two lateral regions; its edges are thickened, and its posterior and external angles are produced backwards. At the anterior end of the median region two simple eyes are situated, and at its sides are two large compound eyes. The sternal surface presents, anteriorly, a flattened *subfrontal area*,

* 'Système Silurien du centre de Bohème.' Tome i. Trilobites. 1852.

† H. Woodward, 'A Monograph of the British fossil Crustacea belonging to the order Merostomata,' 1866.

behind which it is deeply excavated, so that the labrum and the appendages are hidden in a deep cavity formed by its shelving walls. The middle division of the body of *Limulus* exhibits markings which indicate that it is composed of, at fewest, six coalesced somites; its margins are spinose, and its excavated sternal face lodges the appendages of this region.

Fig. 58.

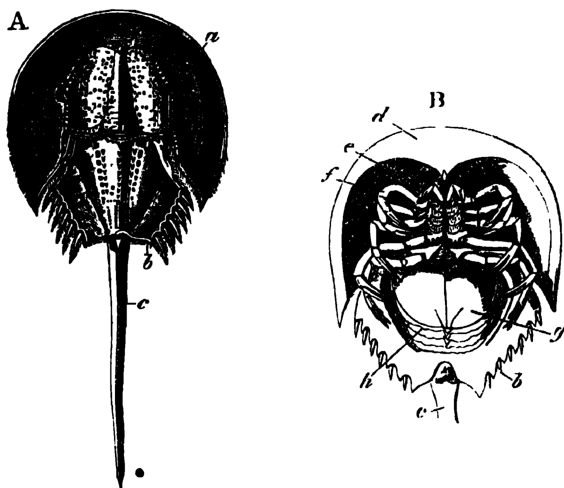


Fig. 58.—A, *Limulus moluccanus* (dorsal view). B, *L. rotundicauda* (ventral view), (after Milne-Edwards): *a*, anterior, *b*, middle division of the body; *c*, telson; *d*, subfrontal area; *e*, antennules; *f*, antennæ; *g*, operculum; *h*, branchiferous appendages.

The terminal division is a long, pointed, and laterally serrated spine, which is termed the *telson*.

The mouth is placed in the centre of the sternal surface of the anterior division; the anus opens on the same surface, at the junction between the middle division and the telson. A moveable, escutcheon-shaped, labrum projects backwards in the middle line, immediately behind the sub-

frontal area (*d*); and, on each side of it, is a three-jointed appendage, the second joint of which is prolonged in such a manner as to form with the third, a pincer or *chela*. The attachment of this appendage is completely in front of the labrum, which separates it from the mouth.

In each of the next five pairs of appendages, the basal joint is enlarged; and, in the anterior four, its inner edge is beset with numerous moveable spines. The attachment of the basal joint of the foremost of these appendages (the second of the whole series) is in front of the mouth; but its prolonged, spinose, posterior and internal angle may be made to project a little into the oral cavity. The basal joints of the following three appendages are articulated at the sides of the mouth, and the inner angle of each is provided with a spinose process which projects into the oral cavity. The second, third, fourth, and fifth appendages in the females are chelate; in the males of most species, the second, and sometimes the third, are not chelate. The large basal joint of the sixth appendage is almost devoid of spines, and bears a curved, spatulate process, which is directed backwards between the anterior and middle divisions of the body. The fifth joint of this limb carries four oval lamellæ. The appendages which form the seventh pair, very unlike the rest, are short, stout, and single-jointed.

The eighth pair of appendages, again, are of a totally different character from those which precede them. They are united in the middle line into a single broad plate, which forms a sort of cover, or *operculum*, over the succeeding appendages, when the animal is viewed from the sternal side. On the dorsal face of this plate are seated the two apertures of the reproductive organs.

From the inner face of the anterior, or sternal, wall of each half of the operculum a strong process arises, and passes upwards to be attached to a corresponding process of the tergal wall of the anterior division of the body. By far the greater part of the large levator muscle of the appendage arises from the tergal wall of the anterior division of the body, and the nerve which supplies

the limb is derived directly from the posterior part of the multiganglionate cord which surrounds the gullet and supplies the appendages which lie in front of the operculum.

The five pairs of appendages which remain resemble the operculum in their general form, and have ascending processes, which are connected with inward prolongations of the tergal wall of the middle division of the body. Their nerves are derived from the ganglia which lie in this region of the body.

Thus there are altogether thirteen pairs of appendages, eight of which are connected with the anterior, and five with the middle division of the body; and the appendages in the region of the mouth are essentially ordinary limbs, the basal joints of some of which are so modified as to subserve manducation.

The determination of the homologies of the parts hitherto spoken of as the anterior and middle divisions of the body, and of their appendages, is a matter of some difficulty; but, on comparing the disposition of the limbs and their nervous supply with what obtains in the higher *Crustacea*, it seems hardly doubtful that the first pair of appendages answer to the antennules; the second, to the antennæ; the third, to the mandibles; the fourth and fifth, to the maxillæ; and the sixth, seventh, and eighth, to the maxillipedes of *Astacus* or *Homarus*; and, in this case, the anterior division is a cephalo-thorax. If the position of the genital openings marks the hinder boundary of the thorax, the middle division of the body represents an abdomen, composed of five somites. But, on the other hand, it may be that the genital organs open in front of the hinder extremity of the thorax, as in female *Podophthalmia*, and that the five somites which form the middle division correspond with the remaining five somites of the thorax of a Podophthalmian. In this case, the region which corresponds with the abdomen in the higher crustaceans is undeveloped.

The alimentary canal of *Limulus* is very peculiarly arranged. The gullet passes directly forwards and upwards, and gradually widens into the stomach, the walls of which

are provided with many longitudinal folds. The pylorus is prolonged into a narrow tube which projects into the intestine. The two biliary ducts on each side are far apart, and branch out into minute tubules, which form a mass occupying the greater part of the cavity of the body. The rectum, a slender canal with plaited walls, and very short, opens into a sort of cloaca situated between the telson and the sternal wall of the abdomen.

The heart, in *Limulus polyphemus*, is an elongated muscular tube, divided into eight chambers, and having as many pairs of lateral valvular apertures. It lies in a large pericardial sinus, which, in its abdominal portion, presents on each side five apertures, the terminations of the branchial veins. The branchiæ consist of numerous delicate semicircular lamellæ, attached transversely to the posterior faces of the five post-opercular appendages, and superimposed upon one another like the leaves of a book.

The nervous system appears, at first sight, to be very concentrated, its principal substance being disposed in a ring, embracing the œsophagus; but, on closer inspection, it is found to consist of an anterior mass, representing the principal part of the cerebral ganglia in most other *Crustacea*, and of two ganglionic cords which proceed from the outer and posterior angles of that mass, and extend as far as the interval between the last and penultimate pairs of appendages. These cords are thick, and lie on each side of the œsophagus, around which they converge, so as to come into close union and almost confluence, immediately behind it. In front of this point, however, they are connected by three or four transverse commissures, which curve round the posterior wall of the œsophagus, and become gradually shorter from before backwards.

The first of these commissures unites the two cords opposite the origin of the nerves to the third pair of appendages, which I regard as the homologues of the mandibles. In front of this point, the cerebral ganglia give off, from their anterior edges, the nerves to the ocelli, eyes, and frontal region; and, from their posterior and under surfaces, those

to the antennules. The nerves to the antennæ arise from the cord close to the outer and posterior angles of the cerebral ganglia, and some distance in front of those to the mandibles. Close behind the latter, arise the large nerves to the fifth and sixth cephalo-thoracic appendages.

The nerves to the rudimentary seventh pair of appendages are slender, and arise rather from the under part of the post-œsophageal ganglia; those which supply the eighth pair of appendages, constituting the operculum, are also slender, and seem to come off from the two longitudinal commissural cords, which connect the post-œsophageal ganglia with those which are situated in the second division of the body, though they are, in truth, only united in one sheath with them for a short distance, and can be readily traced to the post-œsophageal ganglia, internal to the nerves of the seventh pair of appendages. The longitudinal commissures are very long, and are enclosed in a continuation of the same sheath; they pass back into the second division of the body, and there present four ganglionic enlargements, whence the nerves of the post-opercular appendages proceed. The last of these ganglia is much larger than the others, and appears to consist of several confluent masses. The nerves diverge from it in such a manner as to resemble a *cauda equina.*

The reproductive organs of both sexes consist of a mass of glandular cæca, which ramify through the body amidst the hepatic tubules, and eventually open on papillæ situated on the posterior face of the operculum. The males are much smaller than the females, and present, in many species, an external sexual distinction in the peculiarity of their second and third appendages already referred to.

The young of *Limulus* acquires all its characteristic features while still within the egg. The interesting observations of A. Dohrn * have shown that, in an early stage,

* "Untersuchungen über Bau und Entwickelung der Arthropoden." ('Jenaische Zeitschrift,' Bd. vi.) See also the observations of Lockwood and Packard, 'American Naturalist,' vol. iv. 1871, vol. vii. 1873, and 'Memoirs of the Boston Society of Natural

the embryo is provided with the nine anterior pairs of appendages, and is marked out into fourteen somites by transverse grooves upon its sternal face. The body has the form of a thick rounded disk, divided into an anterior shield composed of six somites, and a posterior, likewise shield-shaped region, formed by the union of eight somites. The telson has not made its appearance. In this condition, its resemblance, apart from the limbs, to such a Trilobite as *Trinucleus* is, as Dohrn points out, most remarkable.

The *Xiphosura* were represented in the Carboniferous epoch (*Bellinurus*).

The *Eurypterida* (Fig. 59) are extinct *Crustacea* of Palæozoic (Silurian) age, which sometimes attain a very large size and in many respects resemble *Limulus*, while, in others, they present approximations to other *Crustacea*, especially the *Copepoda*. An anterior, eye-bearing, shield-shaped division of the body is succeeded by a number (12 or more) of free somites, and the body is ended by a broad, or narrow and spine-like, telson. Five pairs, at most, of limbs, provided with toothed basal joints, are attached to the sternal surface of the shield, and the mouth is covered, behind them, by a large oval plate which appears to represent a metastoma (Fig. 59, B *g*.). Some of the anterior limbs are frequently chelate (*Pterygotus*); the terminal joints of the most posterior pair are generally expanded and paddle-like. The integument often presents a peculiar sculpture, simulating minute scales. The sternal surface of one or more of the anterior free somites is occupied by a broad plate, with a median lobe, and two laterally-expanded side-lobes (Fig. 59, B *h*), having a remote resemblance to the operculum of *Limulus*.

The ENTOMOSTRACA.—All the remaining *Crustacea* have completely specialised jaws; and as many as six pairs of appendages may be converted into gnathites.

History,' 1872; with the discussion of the systematic place of *Limulus* by E. van Beneden, 'Journal de Zoologie,' 1872.

In the *Entomostraca*, if the body possesses an abdomen (reckoning as such the somites which lie behind the genital aperture), its somites are devoid of appendages. Moreover,

Fig. 59.

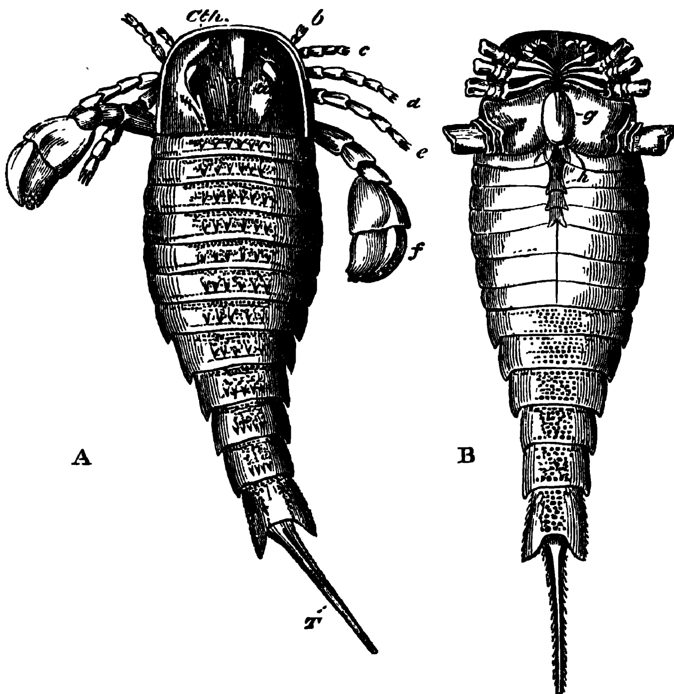


Fig. 59.—*Eurypterus remipes* (after Nieszkowski).*—A, dorsal aspect. B, ventral aspect. *Cth*, the cephalo-thoracic shield bearing *a*, the eyes, and *b*, *c*, *d*, *e*, *f*, the locomotive limbs; T, telson; *g*, the metastoma; *h*, the sternal plates of the anterior free somites.

the somites, counting that which bears the eyes as the first, are more or fewer than twenty. There are never more than

* 'Der *Eurypterus remipes*, aus den obersilurischen Schichten der Insel Oesel.' 1859.

three pairs of gnathites. The embryo almost always leaves the egg in the condition of a *Nauplius*; that is, an oval body, provided with two or three pairs of appendages, which become converted into antennary organs and gnathites in the adult. The division of the *Entomostraca* comprises the *Copepoda*, the *Epizoa*, the *Branchiopoda*, the *Ostracoda*, and the *Pectostraca*.

The COPEPODA.—In these *Entomostraca*, which come nearest to the *Eurypterida*, the cephalic shield, which is discoidal and not folded longitudinally, is succeeded by a certain number of free thoracic and abdominal somites. The antennules and antennæ are large, and, as in the *Eurypterida*, are organs of locomotion and sometimes of prehension. The anterior thoracic members are converted into foot jaws; the posterior serve as paddles, the limbs of each pair being often united together in the middle line, as in *Limulus*. The embryo leaves the egg as a *Nauplius*.

The various species of the genus *Cyclops*, which abound in fresh water, afford excellent illustrations of the structure of the *Copepoda*.

The minute animal (Fig. 60) is shaped something like a split pear, the larger end corresponding with the head, and the convex side with the dorsal surface. The anterior third of the body is covered by a large carapace, which, at the sides, extends downwards as a free fold over the bases of the appendages, but is hardly at all free posteriorly. Anteriorly, in the middle line, it curves forwards and downwards, and is produced into a short rostrum, on each side of which a considerable excavation lodges the base of the long antennule, by the vigorous oar-like strokes of which the animal darts through the water. At the anterior boundary of the head, the double, black, median eye, which, unless very closely examined, appears single, shines through the carapace, and at the sides of the latter, two coiled tubes with clear contents, the so-called *shell-glands*, are seen.

Four distinct and moveable somites succeed the carapace, and gradually diminish in diameter. The body then sud-

denly enlarges, and becomes divided, in the female, into four segments, the last of which gives attachment to two long setose styles, which possibly represent another somite. There is a well-developed and prominent labrum (or conjoined epistoma and labrum) in front of the mouth, and behind it is a bilobed metastoma. The first pair of appen-

Fig. 60.

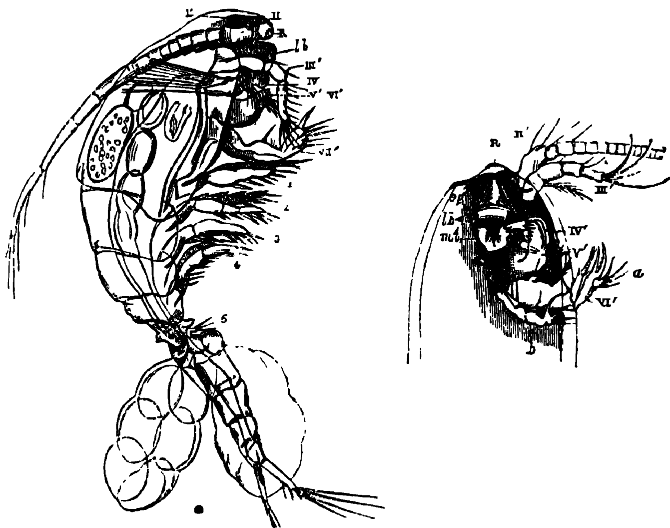


Fig. 60.—*Cyclops.*—Side view of an adult female carrying a pair of ovisacs, and ventral view of the head, showing the labrum, metastoma and appendages of the left side. I′, eye, II′, antennule, III′, antenna, IV′, mandible, V′, first maxilla, VI′, second maxilla (erroneously marked VII′), *a*, outer, *b*, inner division. 1, 2, 3, 4, 5, thoracic limbs. R, rostrum; *lb*, labrum; *mt*, metastoma.

dages are the long and many-jointed *antennules*, which are the chief organs of locomotion. These are succeeded by the short and few-jointed antennæ. The third pair of appendages, or first pair of gnathites, differs from the corresponding limb in *Limulus* in the reduction of the greater part of the appendage to a rudiment terminated by

setæ, while the strong basal part is the principal gnathite or *mandible*. The second pair of gnathites are strong and incurved; following upon these is a third pair of appendages, each divided into two portions, an inner and an outer. The latter is by far the larger, and is so constructed, that the three distal articulations can be bent back upon the proximal ones, and opposed to the internal division, constituting a prehensile organ, the "hand" of Jurine.* Thus the gnathites of *Cyclops* are a pair of mandibles followed by two pairs of maxillæ. At some distance behind the third pair of gnathites the first pair of thoracic appendages is attached to the hinder part of the cephalothorax. Each consists of a two-jointed basal part (*protopodite*), terminated by two three-jointed divisions (*exopodite* and *endopodite*). Three similar pairs are appended to the three anterior free somites, while a fifth rudimentary pair is connected with the next and smallest of these somites. The suddenly enlarged following segment of the body carries the apertures of the reproductive organs in the female, and supports the ovisacs. It is commonly regarded as the first abdominal somite; but, according to Claus, it is composed of two distinct somites, which become united only after the last moult.

The alimentary canal is straight and simple, and without any distinct liver. There is no heart nor any special respiratory organ.

The single ovary, situated in the thorax, is provided with two oviducts, which open on the sides of the coalesced first and second abdominal somites. On the ventral face, between the apertures of the oviducts, is the median aperture of a colleterial gland which secretes the viscid matter which forms the coat of the ovisac. Short lateral ducts connect the gland with the extremities of the oviducts.

* That these are two divisions of the third gnathite, and not two separate appendages, has been demonstrated by tracing out their development. (Claus, 'Organization und Verwandtschaft der Copepoden.' Würzburg Naturwiss. Zeitschrift, 1862.) Under these circumstances I do not know why they should be termed "maxillipedes."

The male is much smaller than the female, and the two enlarged somites of the abdomen remain distinct. There is a single testis provided with two vasa deferentia. A specially glandular portion of the latter secretes the material of the spermatophores, or cases in which the spermatozoa are enclosed. The antennæ are thickened, and provided with a peculiar hinge-joint, by means of which the male firmly seizes the fourth pair of swimming legs of the female during copulation, and then bending up his abdomen, deposits two of the spermatophores on the median opening of the colleterial gland, into which the spermatozoa pass on their way to the oviducts. The gland thus plays the part of a spermatheca. The eggs are carried about in the ovisacs until they are hatched.

The vitellus undergoes complete division, and a morula results, the blastomeres of which soon become differentiated into a superficial epiblast, surrounding a deeper-coloured mass, which gives rise to the hypoblast and mesoblast. The whole embryo then becomes divided by two constrictions into three segments, and the hypoblast arises by delamination around a central cavity, which becomes the alimentary canal. There is a large labrum on the ventral side of the first segment in front of the mouth. The eye appears on the tergal aspect of the most anterior segment, as two pigment-spots which soon coalesce into one; and a pair of jointed setose limbs grows out of each segment. In this *Nauplius*-state the young Cyclops leaves the egg.

The posterior part of the body elongates and becomes divided into the somites of the thorax and abdomen, from which their respective appendages bud out; and these changes are accompanied by exuviation of the cuticle. The three pairs of appendages of the *Nauplius* are converted into the antennules, antennæ, and mandibles of the adult.

There are a few other fresh-water and many marine genera of *Copepoda*. Among the latter, the *Pontellidæ* are remarkable for the separation of that part of the head which bears the antennules and the antennæ, from the rest, a peculiarity to which a parallel can be found only among

the *Stomatopoda*. *Corycæus* has two large, more or less lateral eyes in addition to the median eye, subchelate antennæ, and a rudimentary abdomen. The beautifully iridescent *Sapphirina* has an extremely depressed body, short filiform antennæ, two eyes, and rudimentary gnathites. A short thoracic heart is present in some genera.

The Epizoa.—Insensibly connected by such genera as *Ergasilus* and *Caligus* with the typical Copepods, are a great number of very singular *Crustacea*, which, from their habit of living parasitically upon aquatic animals (whence their vulgar name of "fish-lice"), have received the title of *Epizoa*. *Chondracanthus gibbosus*, commonly found in great abundance on the walls of the branchial chamber of the Fishing-frog (*Lophius piscatorius*), may serve very well as an illustration of the most remarkable peculiarities of this aberrant group.

The female (Fig. 61) is not more than half an inch long, but, posteriorly, two long slender cylindrical filaments, (like the rest of the animal, of a whitish or yellowish colour,) are attached to its body, which is broad and flattened, and as it were crimped at its edges, so as to present two principal transverse folds. The angles of the folds are elongated into lateral processes (*h*, *i*, *f*), and similar processes (*d*, *e*) proceed from the middle line of the body, which by these outgrowths and foldings becomes singularly distorted; and the grotesqueness of the animal's appearance is not a little enhanced by the bowing motion, accompanied by a flapping backwards and forwards of its gouty limbs, which it executes when detached from the integument of the *Lophius*.

The head is expanded into a sort of hood, the convex anterior margin of which bears the antennules and antennæ, the latter being metamorphosed into the strong curved hooks by which the *Chondracanthus* is securely anchored to the infested animal. A subquadrate labrum overhangs the mouth, but does not enclose the mandibles and form a suctorial apparatus, as it does in some *Epizoa*.

The mandibles and the two pairs of maxillæ resemble

curved hooks or claws. Two pairs of appendages (Fig. 61, *b c*), composed each of a protopodite, terminated by an

Fig. 61.

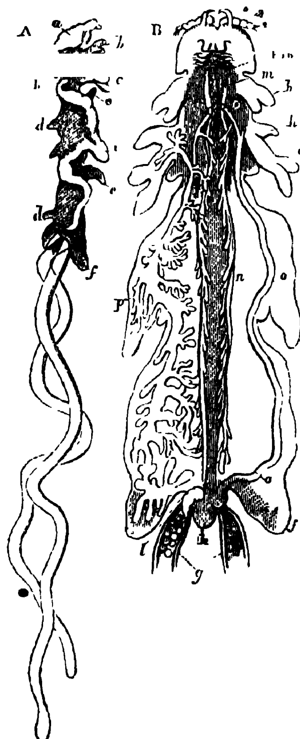


Fig. 61.—*Chondracanthus gibbosus.*—Female: A, lateral view. B, ventral view, enlarged. *a*, head; *b*, *c*, appendages; *d*, median dorsal process; *e*, median ventral processes; *f*, *i*, *h*, lateral processes; *k*, terminal segment, *l*, male; *g*, ovisacs; *m*, *n*, medio-dorsal ovarian tubes; *p*, lateral ovarian tubes; *o*, oviduct. 2, 3, antennules; 4, 5, 6, antennæ, gnathites.

endopodite and exopodite and exhibiting hardly any trace

of articulation, are attached to the anterior part of the body behind the head.

The body ends in a rounded segment, situated in the deep notch between the hindermost marginal processes, and bearing the two projecting vulvæ. Above each of these is a small triangular papillose lobe (Fig. 62, *w*), probably a modified appendage, to which, as we shall see, the male attaches himself, while below them are two other rudimentary appendages (Fig. 62, *y*). The alimentary canal is a straight tube running from the mouth to the opposite extremity of the body. No heart is discoverable, and the nervous system and organs of sense (if any) are equally undistinguishable. The interspace between the alimentary canal and the walls of the body is almost wholly occupied by the ovarium, which consists of four tubes, situated on each side of the intestine, and giving off ramified cæca, in which the ova are developed. Anteriorly, each pair of tubes opens into the oviduct of its side, which passes down along the side of the body to terminate at the vulva. The lower part of the oviduct contains a clear gelatinous substance, and is very similar in aspect to the cement duct of a cirripede; this substance is secreted by the walls of the oviduct, and forms the walls of the ovigerous sac. The latter, as has been stated, has the form of a long cylindrical filament, the upper end of which is firmly held between the prominent lips of the vulva (Fig. 62, *x*).

The male *Chondracanthus* does not attain to a twelfth the length of the female, and looks, at first, like a papilla upon her body near the vulva. On close examination, however, he is seen to be firmly fixed by his antennary hooks to one of the two triangular lobes described above. The hooks are doubtless at first attached to the lobe by muscular contraction; but the connexion once effected seems indissoluble—at least maceration in caustic soda does not cause the male to become detached. It does not appear that more than one male is attached to a female.

The body of the male (Fig. 62) is pyriform, and exhibits indications of a division into six segments beside the head.

The anterior extremity presents a black eye-spot imbedded in its substance, and gives origin to a pair of rudimentary antennules, and to the strong, hooked, prehensile antennæ. Behind and below them is a large labrum and three pairs of hook-like gnathites. These are succeeded by two pairs of subcylindrical appendages, which apparently represent ambulatory limbs.

The caudal extremity is terminated by two styles, and there are two prominent tubercles on the ventral surface of the penultimate somite, in which the genital apertures are seated. The alimentary canal is a delicate, irregular tube,

Fig 62.

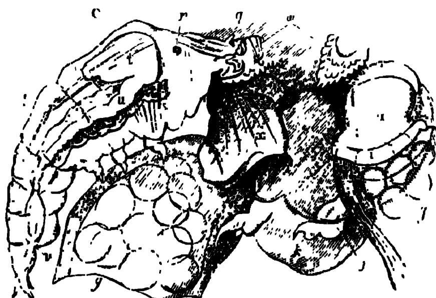


Fig. 62.—C. Male *Chondracanthus*, *in situ*, enlarged: *x*, vulvæ of female; *w*, triangular papillose lobes; *q*, antennæ of male; *r*, eye-spot; *t*, testis; *u*, vas deferens; *v*, genital aperture; *y*, rudimentary appendages of the female; *g*, ovisacs.

having many brownish granules imbedded in its walls. A wide œsophagus is connected with its anterior extremity; but the opposite end appears to be rounded, and to be united with the ventral surface of the integument only by connective tissue. A complex muscular system, composed of striped fibres, is visible through the integument, and the eye-spot seems to be connected with a subjacent ganglionic mass. The body is sufficiently transparent to allow the pulsations of a heart to be seen, but none can be discovered. The testis is a large oval bilobed mass (*t*),

lying like a saddle upon the anterior part of the intestine. From this body a thick vas deferens runs back upon each side of the intestine, and dilates in the penultimate and antepenultimate somites into a thick walled pyriform sac —a sort of vesicula seminalis. The embryo leaves the egg as a *Nauplius*, like that of *Cyclops*.

There are many genera of these parasites, some of which, such as the almost completely vermiform *Lernææ*, deviate even more widely than *Chondracanthus* from the ordinary form of *Crustacea*, while others, such as *Ergasilus* and *Notodelphys*, differ but little from the free *Copepoda*.

In *Caligus*, the labium and metastoma are elongated and united into a tube in which the sharp styliform mandibles are enclosed; and from the prevalence of this suctorial form of mouth in some of the best known species of parasitic *Copepoda*, they are frequently termed "suctorial" crustaceans. Suctorial disks for attachment are developed from the coalesced posterior pair of thoracic members in *Achtheres*; and, in this genus, the head, as a distinct part, becomes almost entirely obsolete.

Argulus, the parasite so common on the Stickleback, is worthy of notice as one of the most curious modifications of the epizoic type.* It is extremely flattened, and is composed of an anterior cephalo-thoracic disk, behind which lies a very short and broad, notched, abdomen. A median styliform weapon lies in a sheath in front of the mouth, and the small mandibles and maxillæ are enclosed in a short tube formed by the labrum and the metastoma. Six pairs of appendages lie behind the mouth, the anterior being metamorphosed into suckers, the next pair into strong limbs with a toothed second joint, and the four others constituting biramous swimming feet. There are two pairs of antennary organs, and two compound eyes. According to Leydig, the males are provided with cups on their

* Claus ('Ueber die Entwickelung, Organization und systematische Stellung der Arguliden,' 1875) has proved the close affinity of *Argulus* with the *Copepoda*, but proposes to regard it as the type of a special group, the *Branchiura*.

penultimate swimming feet; and, during copulation, these are filled with the seminal fluid, which is thus transferred to the vulva of the female, and thence to the spermatheca. The eggs are laid, and not carried about in ovisacs. The larva is provided with two pairs of principal swimming appendages, the future antennæ and the mandibular palps, the latter eventually entirely disappearing. There is a pair of small antennules, a pair of strong legs in the place of the suckers, and, behind them, the rudiments of the prehensile legs and the first pair of biramous appendages, the others being rudimentary.

Notodelphys, which may be found very commonly in the branchial sac of *Ascidians*, closely resembles an ordinary Copepod, except that it becomes much distorted, and that it carries its ova in a chamber formed by the dorsum of the carapace.

However strangely modified the adult form may be (and it must be remembered that it is always the female which undergoes the greatest amount of change), the larvæ of all these epizoic parasites resemble those of the ordinary free *Copepoda* in possessing only two (*Achtheres, Tracheliastes*) or three pairs of appendages, (which appertain to the anterior region of the head); and they are endowed with considerable powers of locomotion.

The BRANCHIOPODA.—The genera *Nebalia, Apus, Branchipus, Limnetis, Daphnia*, and their allies, are usually divided into two orders, the *Phyllopoda* and the *Cladocera*, but these pass into one another so gradually, and have so many structural peculiarities in common, that the subdivision of the group of *Branchiopoda* appears to me to be a step of doubtful propriety. Closely resembling the lower *Podophthalmia*, such as *Mysis*, in some respects, these Crustaceans are invariably distinguished from them by the possession of a greater or less number of somites than twenty; *Nebalia*, which most nearly approximates the higher *Crustacea*, having twenty-two somites. Furthermore the thoracic and abdominal appendages of the *Branchiopoda*

are, in the majority of cases, more or less foliaceous, resembling, in many respects, the anterior maxillipede of an *Astacus*, and being constructed on essentially the same plan.

Apus glacialis (Fig. 63) presents an elongated vermiform body, terminated by two long, multiarticulate, setose styles, and covered anteriorly by a great shield-like carapace, deeply excavated behind. The posterior three-fifths of the carapace are free, and merely overlap the segments of the body; the anterior portion, on the contrary, is united with, and forms the tergal surface of the corresponding region of the head; the free portion of the carapace shelves away laterally from a median ridge, on each side of which a curious concentric marking, indicating the position of the shell gland, (Fig. 63, B, *x*,) is visible. This gland is a coiled tube with clear contents, which, according to Claus, opens on the base of the first pair of thoracic appendages, immediately behind the second maxillæ. Where the free joins the fixed portion of the carapace, the ridge is abruptly terminated by a transverse depression. A little distance in front of this is another deeper transverse groove, close to which, in the middle line, are the two reniform compound eyes, converging towards one another anteriorly (Fig. 63, B, I′).

The ventral surface of the anterior division of the carapace (Fig. 63, C), presents a flattened, semilunar, subfrontal area, as in *Limulus*, behind which it slopes upwards on all sides into the posterior division, thus forming a wide chamber, in which the anterior thoracico-abdominal segments are lodged. In the middle line, the subfrontal plate sends back a long and wide process, moveably articulated with it, and rounded at its free end—the labrum; above and behind which the mouth and gnathites are situated. Behind these follow twenty-six spinulose thoracico-abdominal segments; the anterior twenty of which bear the swimming feet, while the twenty-sixth, much larger than the others, is produced into an incurved point posteriorly, and carries the anus and the terminal setæ.

The compound eyes, as has been said, are seated upon the upper surface of the anterior division of the carapace. On

the under surface, just above and behind the posterior boundary of the subfrontal area, and on each side of the labrum (Fig. 63, C, *lb*), is a delicate jointed filament—the antennule (Fig. 63, C, II′). Behind this, Zaddach found in some specimens of *Apus cancriformis*, a second very small filament, the rudiment of the antenna, which in the larva is so large and important an organ; but I have observed nothing of the kind in *A. glacialis*. On each side of the labrum is a large, convex, strong, toothed mandible, and the aperture of the mouth is bounded posteriorly by a profoundly divided plate, the *metastoma*. Succeeding this are two pairs of small maxillæ, the second pair being foliaceous. and almost rudimentary. Behind these appendages, a cervical fold marks off the boundary between the head and the thorax, and at the same time corresponds with the commencement of the free portion of the carapace. Whether the carapace is also to a certain extent attached to the first thoracic somite, as Grube states,* or whether it is entirely cephalic, as Milne-Edwards considers, is a point upon which I have been able to come to no very clear determination; indeed, it is a question rather for the embryologist than the anatomist.

Of the twenty pedigerous segments, the first eleven have each one pair of appendages; but, behind the eleventh, each segment gives attachment to a gradually increasing number of limbs, so that the twentieth carries five or six pairs. Altogether twenty-eight pairs of appendages are attached to these nine posterior thoracic segments; these, added to the eleven preceding, make thirty-nine appendages in all. While each of the anterior eleven segments must be regarded as single somites, the nature of the posterior ones is open to doubt; they may be single terga, the sterna and appendages of which have multiplied; or, more probably, they each represent a number of coalesced terga.

Each appendage consists of three divisions—an endopodite, exopodite, and epipodite, supported on a protopodite or basal division (Fig. 63, D, E, F). The latter consists of three

* 'Bemerkungen über die Phyllopoden,' p. 81.

Fig. 63.

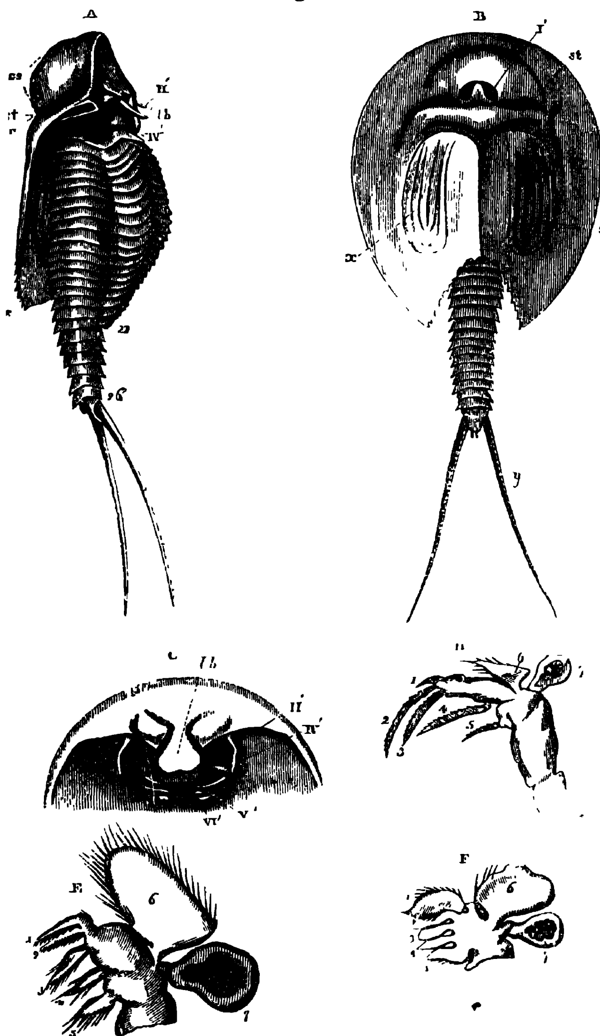


Fig. 63.—*Apus glacialis.*—A, lateral view, with the right half of the carapace cut away. B. Dorsal view. C. Anterior part of the body, ventral aspect. D, one of the anterior, E, one of the middle, and F, one of the posterior limbs, without their coxopodites. *x*, convoluted "shell gland" in the carapace; *y*, caudal filament; *lb*, labrum. 1, 2, 3, 4, Endopodite. 6 Exopodite. 7. Epipodite or branchia. I', eye; II', antennule; IV', labrum; V', VI', maxillæ.

joints—a coxopodite produced internally into a strongly setose prominence (not represented in the figures), a basipodite, and an ischiopodite, the latter elongated internally into a lanceolate process, and bearing on its outer side two appendages, of which the proximal — the epipodite or branchia (Fig. 63, D, E, 7)—is pyriform and vesicular in specimens preserved in spirit. The distal appendage, which appears to represent the exopodite (6), is a large flat plate, provided with long setæ on its margin.

The endopodite consists of four joints, the two proximal ones being much the longer, and, like the penultimate, giving off internally a long process. Finally, the terminal joint is claw-like and serrated on its concave edge.

The average form of these appendages is represented by (E) taken from the middle of the series; anteriorly the limbs become more slender and leg-like (D); posteriorly, on the other hand, they are completely foliaceous, as (F); but the same elements are recognisable throughout.

The eleventh pair of appendages alone depart, in any important respect, from the rest of the series, each of these being modified so as to serve as a receptacle for the ova. To this end the joints of the endopodite are greatly expanded, and converted into a hemispherical bowl; the exopodite, metamorphosed into another such bowl, shuts down over the endopodite; and, into the box thus formed, the ova are conducted by means of the oviduct, which opens into it.

On the dorsal surface of each side of the terminal segment of the body there is a tubercle produced into five spines anteriorly, and carrying, posteriorly, a long and delicate setigerous filament (Fig. 63, B, *g*).

The alimentary canal of *Apus* is very simple, consisting

of a vertically ascending œsophagus, which bends back into the small stomach, situated immediately behind the compound eyes, in the middle of the region bounded by the two transverse furrows on the dorsum of the carapace; from the hinder end of the stomach the straight intestine passes back to the anus, which is seated beneath the terminal segment. The liver consists of cæca, which branch off from the stomach and lie, on each side of it, in the head. Zaddach describes a pair of glands which he regards as salivary, placed above, and opening into, the stomach itself, like the salivary glands of the Scorpion.

The heart occupies the tergal region of the eleven anterior thoracic somites, presenting as many chambers, with lateral venous apertures.

The nervous system consists of a quadrate cerebral mass, placed immediately under the compound eyes, and giving off large nerves to them and to the remains of the single eye of the larva, which lies in front of their anterior extremities. Commissures pass downwards and backwards on either side of the œsophagus, and connect the cerebrum with a chain of numerous ganglia placed on the median line of the ventral surface. It is worthy of remark, that the antennary and antennulary nerves are given off from the commissures, far behind the chief cerebral mass.

In the female, the ova are developed in the cæcal branches of two long tubes, situated one on each side of the body, and opening, as above described, in the eleventh pair of appendages. *Apus* usually propagates agamogenetically, and the examination of thousands of individuals, extending over more than thirty years, failed to reveal to Von Siebold the existence of a male form. In 1856, however, Kozubowski * discovered a small proportion of males (16 in 160), among the specimens taken in the neighbourhood of Cracow; and near Rouen, in 1863, Sir John Lubbock found the largest proportion of males to females yet known, viz., 33 in 72. On the other hand, between 1857 and 1869, Von

* "Ueber den männlichen *Apus cancriformis*." ('Archiv für Naturgeschichte,' 1857.)

Siebold examined many thousands of specimens of the Bavarian *Apus* without finding a single male.*

The testis is similar to the ovary in form, and its duct opens upon the eleventh pair of appendages, as in the case of that of the female organs. The spermatozoa are oval and without motion.

The young *Apus* (*cancriformis*), when just hatched, is a *Nauplius*. The body is oval, indistinctly divided into a few segments, and entirely destitute of appendages, except a shorter anterior, uniramous, and a longer posterior, biramous, pair of oar-like organs, situated at the anterior extremity, on either side of the single median eye. The carapace is rudimentary, and there are no caudal filaments. The little animal soon casts its skin, and the mandibles, which are provided with long palps, make their appearance.† With successive ecdyses, the larva assumes more and more the form of the adult, and acquires the pair of compound eyes; the anterior pair of appendages being converted into the antennules, the posterior pair disappearing, or remaining as rudimentary antennæ, and the mandibular palps also vanishing.

Singular and highly instructive modifications are exhibited by the other genera of the *Branchiopoda*, such as *Nebalia*, *Branchipus* (*Cheirocephalus*), *Limnetis*, and *Daphnia*.

In *Daphnia* and its allies (Fig. 64), the thoracic members are reduced to six, five, or even four pairs, some or all of which may take the form of ordinary limbs; the abdomen is rudimentary; the heart is short; and the carapace presents a posterior division (*omostegite*), obviously developed from the anterior thoracic somites, the lateral halves of which are deflexed so as to resemble a bivalve shell, into which the hinder part of the body can be withdrawn. The anterior division of the carapace (*cephalostegite*) in *Daphnia* has, on the contrary, the same structure as the corresponding part

* 'Beiträge zur Parthenogenesis der Arthropoden,' 1871. It appears that, in *Apus*, the impregnated ova alone give rise to males.

† According to Claus's recent investigations, this third pair of appendages is present from the time the young *Apus* leaves the egg.

of the carapace of *Apus*, but the compound eyes, represented by a single mass, are situated at the anterior extremity of the head, rather than on its upper surface, and the single eye is quite distinct, and far posterior to them (Fig. 64, B, I', II''). The antennules (Fig. 64, A, II') are small, rudimentary, and placed at the sides of the produced frontal

Fig. 64.

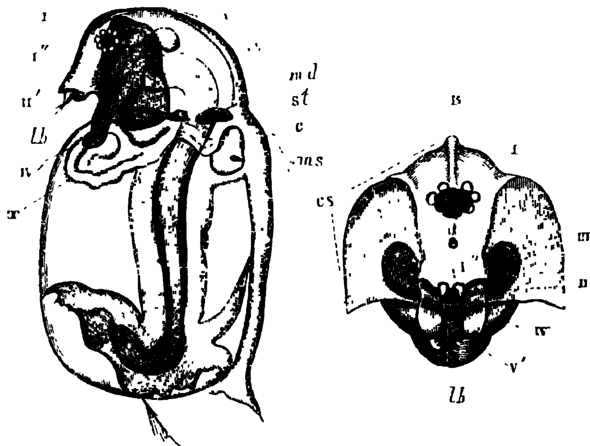


Fig. 64.—*Daphnia*.—A. Side view; the appendages not figured except II', the antennules; IV', the mandibles; and V', the maxillæ. III'. The place of attachment of the antennæ. B. Front view of head.
cs, cephalostegite, or that part of the carapace which covers the head; *ms*, omostegite, or thoracic portion of the carapace; *c*, heart; *st*, cervical depression; *lb*, labrum; I', compound eye; II', simple eye; *a*, the 'shell-gland,' which opens behind the maxillæ.

rostrum, but the antennæ are very large, and constitute the principal locomotive organs. The posterior, or second, maxillæ are obsolete. In *Evadne*, *Polyphemus*, *Sida* and other genera, sucker-like organs of adhesion are situated on the anterior region of the carapace. The eggs are developed in the cavity of the carapace, and the embryos pass

directly into the form of the parent, except in *Leptodora*, where they are, at first, *Nauplius*-like.

Limnetis and *Estheria* present a *Daphnia*-like carapace, though more completely bivalve, combined with the numerous segments of the body and the foliaceous appendages of the typical Phyllopods (Fig. 65).

Nebalia has a large carapace, provided with a moveable rostrum, like that of *Squilla*, and arising entirely from the head, which is remarkable for its very slight sternal flexure. In this genus, the eyes are large and pedunculated; there are well-developed antennules, antennæ, mandibles, and two pairs of maxillæ, the anterior of which ends in a long palp.

Branchipus, finally, developes no carapace either from the head or the thorax, the segments of the latter being entirely free, while the former is similar in shape to that of an Insect, or Edriophthalmous Crustacean, and carries two large stalked eyes, two antennules (singularly modified in the male), two antennæ, a pair of mandibles, and two pairs of maxillæ.

In *Estheria* and *Limnetis*, the males are met with in full proportion to, and may be even more numerous than the females. No males are known in *Limnadia gigas*, although thousands have been examined, while, in *L. Stanleyana*, more males than females have been found. In *Branchipus*, males are fewer than females; in *Artemia*, they occur only at rare intervals. In *Daphnia*, the males are few, and appear only at certain seasons of the year. But notwithstanding the rarity or absence of the males in many of these genera, reproduction proceeds with great rapidity. The ova are capable of development without fecundation; and isolated females of the genus *Daphnia* will thus go on producing broods for generation after generation, without any known limit.

Under certain circumstances, however, bodies of a different nature from these "agamic ova," as they have been well

[1] "Ueber die Gattungen *Estheria* und *Limnadia*." ('Archiv für Naturgeschichte,' 1854.)

termed by Sir John Lubbock,* are developed within the ovary, the substance of which acquires an accumulation of strongly refracting granules at one spot, and forms a dark mass, the so-called "ephippial ovum." When fully formed, two of these bodies pass into the dorsal chamber of the carapace, the walls of which have, in the meantime, become

Fig. 65.

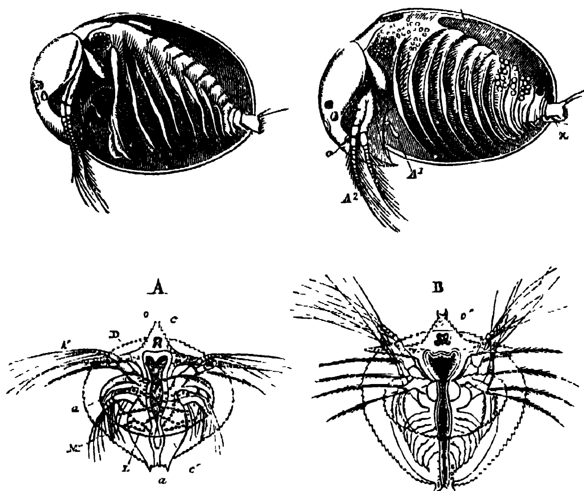


Fig. 65.—*Limnetis brachyurus* (after Grube).—The upper left-hand figure is the male, the other the female; one valve of the carapace in each case being removed. A^1. Antennules. A^2. Antennæ. A. Young larva. B. The same further advanced. c. Head. o. Eye. d. Carapace. c'. Body. A'. Antennæ. M. Mandibles. a'. Great plate (labrum ?) which covers the mouth.

altered. The outer and inner layers of the integument acquire a peculiar structure, a brown colour, and a more firm consistency, over a large saddle-like area. When the

* "An Account of the two methods of Reproduction in *Daphnia*, and of the structure of the ephippium." (Transactions of the Royal Society, 1857.)

next moult takes place, these altered portions of the integument, constituting the "ephippium," are cast off, together with the rest of the carapace, which soon disappears, and then the ephippium is left, as a sort of double-walled spring box (the spring being formed by the original dorsal junction of the two halves of the carapace), in which the ephippial ova are enclosed. The ephippium sinks to the bottom, and, sooner or later, its contents give rise to young *Daphniæ*.

Jurine's and Sir J. Lubbock's researches have proved that the development of the ephippial ova may commence without the influence of the male, and they seem to indicate that these ova may even be fully formed and laid without the male influence. On the other hand, there appears, under ordinary circumstances, to be a certain relation between the complete development of ephippial ova and the presence of males; and, as yet, no ephippial ova produced by virgin females have been directly observed to produce young. The question, therefore, seems to stand thus, at present: the agamic ova may *certainly* be produced, and give rise to embryos, without impregnation; the ephippial ova may *certainly* be produced without impregnation; but whether impregnation is or is not absolutely necessary for their further development, there is, at present, no evidence to show.

The great majority of the *Branchiopoda* inhabit fresh waters. *Artemia*, however, delights in brine pools. The genus *Estheria* is of Devonian age, and it seems probable that the Silurian *Hymenocaris* and its allies were related to *Apus*.

The OSTRACODA.—This group contains several genera of both recent and fossil *Crustacea*, for the most part of very small size, and distinguished by their hard, often calcified, and completely bivalve shell, provided with a distinct hinge. The valves of this shell consist of the lateral moieties of the carapace; they are commonly unequal and unsymmetrical, and present a peculiar ornamentation. The shell gland is very small. The *Ostracoda*

are also remarkable for the extremely rudimental condition of their abdomen, and for the paucity of their thoracic appendages, which instead of being foliaceous, are strong and subcylindrical, like the ambulatory legs of the higher *Crustacea.*

The cephalic flexure is as well marked as in the highest *Crustacea*, so that the eye, obscurely divided, and median in *Cypris* (Fig. 66, A), but double and lateral in *Cythere* (B), is situated in the upper part of the anterior region of the body. The antennules and antennæ, attached to their respective somites, the sterna of which constitute the anterior boundary of the body, are similar in form and function to ambulatory limbs. The ducts of a peculiar gland open, according to Zenker, at the end of the strong spine with which the antenna of *Cythere* is provided. The labrum is conspicuous, and the mandibles are strong, and possess a well-developed palp. The first maxilla is provided with a large foliaceous setose appendage (epipodite?) The second maxilla in *Cythere*, is represented by the first of the three pairs of ambulatory limbs (Fig. 66, B, *e*, *e*, *e*), present in this genus. In *Cypris*, which possesses a second pair of maxillæ, there are only two pairs of ambulatory limbs (Fig. 66, A, P. I. II.). The apertures of the reproductive organs, provided in the male with a wonderfully complex, horny, copulatory apparatus (described with great minuteness by Zenker), are situated between the last pair of thoracic members and the large caudal hooks.

Strong adductor muscular bundles pass from one valve of the carapace to the other, and leave impressions discernible from without, the form and arrangement of which furnish valuable systematic characters.

The alimentary canal of the *Ostracoda* is provided anteriorly with an apparatus of hard parts, resembling in many respects the gastric armature of the *Isopoda*, and gives origin to two hepatic cæca. *Cypris* and *Cythere* have no heart; but, in *Cypridina*, *Conchœcia* and *Halocryptis* there is, according to Claus, a short saccular heart with one anterior and two lateral apertures. The nervous

system is difficult to make out; but, in *Cythere lutea*, the same observer found a large cerebral ganglion in front of the mouth, whence filaments passed to an ophthalmic ganglionic mass, and to the antennary organs. A double ganglion, behind the mouth, supplies the gnathites; three ganglia, situated in the thorax, send filaments to its appendages, and a terminal ganglion supplies the caudal appendage and genitalia. In the female, the ovaries lie in the valves of the carapace, and terminate in oviducts which open by distinct apertures in front of the caudal appendage. Immediately anterior to them are the openings of two

Fig. 66.

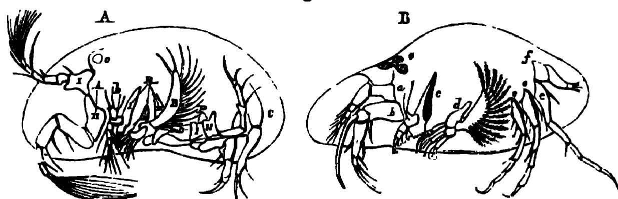


Fig. 66.—A. *Cypris*.—A. I. II. Antennules and Antennæ. M. I. II. III. Mandibles and Maxillæ. P. I. II. Thoracic members. *c*. Caudal extremity. *b*. Mandibular palp. *o*. Eye. B. Maxillary appendage.
B. *Cythere*.—*o*. Eye. *a*. Antennule. *b*. Antenna. *c*. Mandible. *d*. First maxilla. *e*. *e*. *e*. Second maxilla and two thoracic members. *f*. Caudal extremity. (After Zenker.)*

horny canals, called vaginæ by Zenker, each of which is continued into a long convoluted transparent tube, and eventually terminates in a large vesicle, the spermatheca, into which the spermatozoa of the male are received.

In the males, the antennæ, the second maxillæ, or some of the thoracic limbs, are modified in such a manner as to enable them to seize and hold the females. The testes are elongated cæca in *Cypris*, globular vesicles in *Cythere*, and communicate with a long vas deferens, which opens into

* "Monographie der Ostracoden." ('Archiv für Naturgeschichte, 1854.)

the copulatory apparatus. In *Cypris*, a very singular cylindrical mucous gland is connected with the vas deferens; but perhaps the most remarkable peculiarity about the genital apparatus in the male consists in the size of the spermatozoa, which in *Cypris ovum* are, according to Zenker, more than three times as long as the body. They possess a spirally-wound coat, and are totally deprived of mobility.

The *Ostracoda* either attach their eggs to aquatic plants, or carry them about between the valves of the carapace.

Claus * has worked out the development of *Cypris*, which passes through nine successive stages, distinguished from one another, not merely by the shape of the carapace, but by the number and form of the limbs. An ecdysis of the chitinous cuticle of the body and carapace terminates each stage of development. When the *Cypris* leaves the egg, it resembles a *Nauplius*, in possessing a single median eye and only three pairs of limbs (the future antennules, antennæ, and mandibles); but none of these are divided into two branches. The body is laterally compressed and has a bivalve carapace.

The changes undergone by the marine *Ostracoda* after they leave the egg are much less marked.

Fossil *Ostracoda* abound in strata of all ages, from the older palæozoic formations onwards; and, so far as the characters of the carapace furnish evidence, the most ancient forms differed very little from those which now exist.

The PECTOSTRACA (*Rhizocephala* and *Cirripedia*) leave the egg as a *Nauplius*, provided with three pairs of limb-like appendages, of which the anterior pair are simple, while the two posterior pairs are bifurcated (Fig. 68, A). An additional pair of filiform appendages subsequently makes

* 'Entwickelungsgeschichte von Cypris' (1868); and 'Grundzüge,' p. 487.

its appearance in front of the undivided pair of members, in most cases; and there is a discoidal carapace, the antero-lateral angles of which usually become greatly produced. Subsequently, the carapace becomes bivalve (as in many *Phyllopoda*, and in the *Cladocera* and *Ostracoda*), and the anterior undivided pair of limbs are converted into relatively large, jointed appendages, provided with a sucker-like organ. The thorax grows and usually developes six pairs of appendages.

Finally, the bivalve-shelled larva fixing itself by the suckers of its anterior limbs, the præ-oral region of the head becomes enlarged, and is converted into the base, or peduncle, in ordinary Cirripedes; while it gives off the root-like processes which grow into the tissues of the animals on which the *Rhizocephala* are parasitic. The *Pectostraca* are almost all hermaphrodite, a condition which is very exceptional among Arthropods. They possess no heart.

The CIRRIPEDIA.—It can hardly be a matter of reproach to the older naturalists if they failed to discover the affinity connecting the sedentary "Acorn-shells" of a rocky coast with the active Shore-crab which runs amongst them; or if they classed the Barnacles with *Mollusca*, instead of admitting them to that place amidst the *Crustacea* which is now assigned to them by every naturalist of competent judgment. Nothing, in fact, at first sight, is less suggestive of a Crustacean than a *Balanus*, or a *Lepas*; the former firmly fixed by the base of its multivalve conical shell, the latter by its fleshy and contractile peduncle; the only sign of life in either being the alternate protrusion and retraction from the valvular opening of the animal's case of a bundle of curved filamentous cirri, which sweep with a brushing motion through the water, and scoop the floating nutritive matters towards the mouth.

The valves through which the cirri make their egress are strengthened, in both *Balanus* and *Lepas*, by four calcified pieces, two on each side; those of each half being

united together by an oblique suture, or by a regular articulation; while the two pieces of opposite sides are connected only along one margin, either immediately (*Balanus*), or by means of an intermediate piece (*Lepas*).

The upper, or distal, pieces are termed the *terga*, the lower, or proximal, pieces the *scuta*, the intermediate piece is the *carina*. In *Lepas*, there are no other hard external pieces; but, in *Balanus*, the conical shell, into which the valves can be more or less completely retracted, is composed of six portions or *compartments*. Of these, one is situated on the same side as the opening between the valves and another at the precisely opposite point, or on the same side as the line of union of the valves. The latter is the homologue of the intermediate piece, or *carina*, in *Lepas*; the former, in *Balanus*, consists of three pieces united together, the median *rostrum* and the two *rostro-lateral* compartments. On each side of the carina is a compartment termed *carino-lateral*, and between them and the complex rostrum lies a *lateral* compartment.

If the shell consisted of its eight typical pieces (as it does in the genus *Octomeris*), it would be found that each presented a triangular free middle portion and two lateral wings. The former is always termed the *paries*, but the latter receive different names, according as they overlap or are overlapped by others. In the former case, they are termed *radii*, in the latter, *alæ*. Thus, typically, the carinal and the rostral compartments are overlapped on both sides, and their wings are consequently both alæ; the lateral and carino-lateral compartments are overlapped on one side, and overlap on the other, hence they have an ala on one side, a radius on the other; while the rostro-lateral compartment overlaps on both sides, and hence its wings are both radii. In *Balanus*, however, the rostrum and rostro-lateral compartments, being replaced by a single compartment formed by their confluence, this piece has radii on both sides.

Different as is the appearance of *Lepas* from that of *Balanus*, they closely resemble one another in essential

structure. Thus, to commence with *Lepas*. On cutting away the scutum and tergum of one side (Fig. 67, B), the hinder part of the body of the animal is seen within the sac of the *capitulum*, formed by the valves of the shell, to which it is attached only ón the rostral side and inferiorly by a comparatively narrow isthmus. Immediately behind this point the body widens, to constitute what Mr. Darwin* has termed the *prosoma*, but the thoracic segments, which succeed the prosoma, gradually taper posteriorly. Six pairs of appendages (*a*) are attached to the thorax, each limb consisting of a basal joint (protopodite), terminated by two long multi-articulate cirri, the representatives of the endopodite and exopodite; and a rudimentary abdominal segment, terminated by two short caudal appendages, succeeds the thorax, and is produced in a long setose annulated penis (*f*). Filamentous appendages depend from some of the thoracic somites, and, projecting from the inner wall of the sac on each side, is a triangular process, the *ovigerous frœnum* (*m*).

The mouth is situated at the posterior part of a protuberant mass, seated on the rostral face of the prosoma. This is principally composed of a large, bullate labrum, behind which are a pair of mandibles with large and setose palps, and two pairs of maxillæ. Anteriorly, the prosoma passes by a narrow isthmus into the rostral part of the peduncle, into which it, as it were, expands; while the posterior margins of the peduncle become continuous with the walls of the sac.

The extremity of the peduncle is fixed by a peculiar cementing substance to the body to which the *Lepas* adheres; but, if it be carefully detached, there will be found connected with the rostral portion of the surface a pair of very minute, singular-looking, organs, consisting of two proximal joints, succeeded by an articulation which is dilated into a sucker, and terminated by an elongated setose joint (Fig. 67, A, B, *l*). These are the remains of the anterior appendages of the larva.

* 'Monograph of the Cirripedia,' 1851, 1854.

From what has been said, it follows that the fixed end of the peduncle is, in fact, the anterior extremity of the body of the *Lepas*, and that a Barnacle may be said to be a Crustacean fixed by its head, and kicking the food into its mouth with its legs.

Fig. 67.

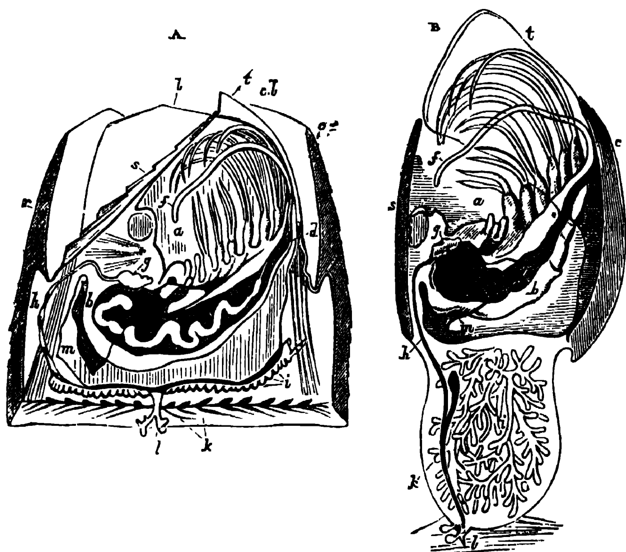


Fig. 67.—A. Diagrammatic section of *Balanus*; B, of *Lepas*.—*a* is placed in the cavity of the sac, and lies over the labrum; *b*, prosoma; *c*, carina; *c*, *l*, carino-lateral compartment; *l*, lateral compartment; *r*, rostrum; *s*, scutum; *t*, tergum; *f*, penis; *g*, gut-formed gland; *h*, duct connecting this with *i*, *k*, cement duct and glands; *l'*, antennæ; *i*, peduncular or ovarian tubules; *m*, ovigerous frænum; *d*, anus.

The mouth in *Lepas* looks towards the posterior extremity of the body, and leads into a tubular œsophagus, which passes forwards, and opens by a wide superior extremity into the globular stomach. From this point, the alimentary

canal bends back upon itself, and gradually narrows into the intestine, which terminates in the anus, situated at the extremity of the abdomen, on the tergal side of the penis. Two considerable branched cæca, probably hepatic, proceed as diverticula from the stomach, corresponding very closely in position with those of *Daphnia.* No heart or other circulatory organs are known to exist; and it may be doubted if the ovigerous fræna of *Lepas* exert, as they have been supposed to do, a branchial function.

The nervous system consists of a pair of cerebral ganglia situated in front of the œsophagus, and connected by long commissures with the anterior of five pairs of thoracic ganglia, whence nerves are given off to the limbs. In the middle line, the cerebral ganglion gives off two slender nerves, which run parallel with one another in front of the stomach and enlarge into two ganglia, whence they are continued to a double mass of pigment, representing the eyes. From the outer angles of the cerebral ganglion arise the large nerves which proceed into the peduncle and supply the sac. These appear to correspond with the antennary and frontal nerves of other *Crustacea;* and Mr. Darwin describes an extensive system of splanchnic nerves.

Lepas, like the majority of the *Cirripedia,* is hermaphrodite. The vesiculæ seminales are readily seen in fresh specimens, as white cords distended with spermatozoa, which run from the canal of the penis, into which they open, forwards, on each side of the body, to the prosoma, where they end in dilated extremities, which are connected with a multitude of ramified cæca forming the proper testis.

The ovaries are ramified tubes provided with cæcal dilatations, and lodged in the peduncle. The oviducts pass into the body, and, according to Krohn, terminate in apertures situated on the basal joint of the first pair of cirri.* Two 'gut-formed' glands, as they are termed by Darwin, lie, one on each side of the stomach, and are probably

* The position of these apertures corresponds with that of the openings, supposed to appertain to the shell-glands in *Limnadia* and *Apus.*

accessory glands of the reproductive organs, analogous to those which secrete the walls of the ovisac in the *Copepoda.*

The mode of exit of the ova from the ovary is not certainly known, nor is the place of their impregnation ascertained; but they are eventually found cemented together by chitin into large lamellæ, which adhere to the ovigerous fræna, and, ordinarily, at once strike the eye when the capitulum of a Cirripede is opened.

Yelk division is complete, and the embryo attains to its earliest larval condition within the egg. If a series of the fresh ovigerous lamellæ be taken and pulled to pieces with

Fig. 68.

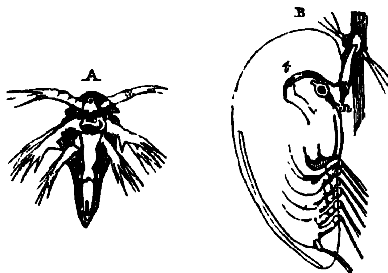


Fig. 68.—A. Larva of *Balanus balanoides* on leaving the egg (after Spence-Bate). B. Attached pupa of *Lepas australis* (after Darwin): *n*, antennary apodemes; *t*, gut-formed gland, with cement duct running to the antenna.

needles in a watch-glass full of sea-water, one is pretty sure to be found whence a number of active little *Nauplius*-like animalcules are set free (Fig. 68, A). Each presents a somewhat triangular body, produced in the middle line posteriorly and at its anterior lateral angles. The mouth is situated on a proboscidiform projection placed nearly in the centre of the body, and in the midst of three pairs of natatory limbs, of which the two posterior pairs have bifid extremities. In front of the mouth, either in this stage, or after one or two moultings, two filaments are often developed. A single eye-spot is situated in front of the bases

of the anterior appendages. After moulting several times, the larva assumes a new form, passing into its second stage. The carapace is now oval and compressed, so as more nearly to resemble that of a *Daphnia* or *Cypris*. There are two eyes. The first pair of swimming appendages of the *Nauplius* are converted into antenniform organs, each provided with a sucker, and the rudiments of the six pairs of cirri make their appearance behind the mouth.*

In the third stage, the larva is, as Mr. Darwin states, "much compressed, nearly of the shape of a *Cypris* or mussel-shell, with the anterior end the thickest, the sternal surface nearly or quite straight, and the dorsal arched. Almost the whole of what is externally visible consists of the carapace; for the thorax and limbs are hidden and enclosed by its backward prolongation; and, even at the anterior end of the animal, the narrow sternal surface can be drawn up, so as to be likewise enclosed." The larva, in this stage, is provided with two large compound lateral eyes, while the median eye is arrested in its development. The oral tubercle exhibits all the gnathites of a Cirripede, but they are covered by an imperforate integument, so that this "locomotive pupa," as Mr. Darwin terms it, is unable to feed. There are six pairs of legs, and the thorax ends in an abdomen, consisting of three somites terminated by two caudal appendages. There is no penis. The most remarkable structures in the pupa, however, are the "gut-formed glands," which are already well developed, and from which the cement ducts can be traced to the disks of the antenniform organs, on the faces of which they open. The pupa, after swimming about for awhile, at length selects its permanent resting-place, to which it adheres, at first, only by the action of the suctorial disks. The temporary attachment, however, is speedily converted into a persistent one, the cement pouring out from its excre-

* According to Claus ('Grundzüge der Zoologie,' 3te Auflage, p. 460), the second pair of appendages disappears, and the third gives rise to the mandibles. In this case the antennary organs represent antennules, and the limbs of the Cirripede *Nauplius* correspond with those of the Copepod and Branchiopod *Nauplius*.

tory apertures on the disks, and firmly gluing them and the anterior end of the body down to the surface on which they rest.

Coincidently with these changes, several other important alterations take place, during the passage of the locomotive pupa into the fixed young Cirripede. The compound eyes are moulted, and with them the antennary apodemes, furnished by the integument of the deep fold which separates that part of the body of the pupa which corresponds with the beak of a *Daphnia*, or of a *Limnetis*, from the prosoma. The fold is thus enabled to straighten itself; and, as a consequence, the carapace of the Cirripede, instead of remaining more or less parallel with the surface of attachment, becomes perpendicular to it. Again, in the pupa, the axis of the carapace and that of the body are identical in direction; but, during the last moult, the chamber of the carapace extends forwards far more on the tergal than on the sternal side, separating the tergal part of the prosoma from the "beak," with which it was at first continuous, and thus allowing the body of the Cirripede to take its final position, which is nearly transverse to the axis of the carapace.

The terga and scuta now appear as horny thickenings, and, afterwards, as calcifications in the wall of the capitulum. The fræna and the penis make their appearance, and the genitalia become developed in the prosoma and in the peduncle, which is produced by the gradual elongation of the "beak" of the pupa.

With the assumption of its perfect form, the Cirripede ceases to moult its carapace, ecdysis being hereafter confined to the inner lining of the sac, and to the integument of the contained body.

Such is the structure and development of a typical pedunculate Cirripede. In other genera, such as *Pollicipes*, calcareous plates are developed on the peduncle, foreshadowing the compartments of the sessile forms. The latter, of which *Balanus* may be regarded as the type, differ in structure from *Lepas* in no very essential particular. The peduncle, very short and broad, instead of slender and elon-

gated, is encased by its compartments, and is sometimes fixed by a shelly basis. The arrangement of the layers of cement is often extremely complicated; the scuta and terga are articulated together; the fræna are much larger organs, and possibly subserve the respiratory function; the thoracic ganglia are concentrated into a single mass; and the cementing apparatus is much more complicated.

The pedunculate and sessile *Cirripedia*, taken together, constitute by far the largest of the three great groups which Mr. Darwin recognises; namely, the *Thoracica*, characterised by having limbs attached to the thoracic somites, while the abdomen is rudimentary.

The second group, the *Abdominalia*, contains only one genus, *Cryptophialus*, (Fig. 69, 5, 6) which has no thoracic limbs, but is provided with three pairs of abdominal appendages. The larva is very imperfect in its first and second changes, which are undergone within the sac of the parent.

The third group, *Apoda*, likewise contains only one genus, the remarkable *Proteolepas* (Fig. 69, 7), which is devoid of either thoracic or abdominal limbs; it has a vermiform body, and a rudimentary peduncle, represented by two threads terminated by the characteristic antenniform organs.

In the great majority of the *Cirripedia* the sexual apparatus is disposed as in *Lepas*, but *Cryptophialus* and *Alcippe* are unisexual, the male differing very widely in form and size from the female (Fig. 69, 3, 6).

The *Balanidæ*, or sessile Cirripedes, all present the normal sexual relations; but the other division of the *Thoracica*, the *Lepadidæ*, contains two genera, *Ibla* and *Scalpellum*, which not only possess species having the sexes in distinct individuals, but others presenting the unique combination of males with hermaphrodites. Thus, *Scalpellum vulgare* is hermaphrodite, possessing well-developed male and female organs. Nevertheless, on the inner side of the occludent margin of its scutum there is a fold, over which and imbedded in the spinose chitinous border of the scutum, a

minute, oval, sac-like creature is commonly found, firmly at-

Fig. 69.

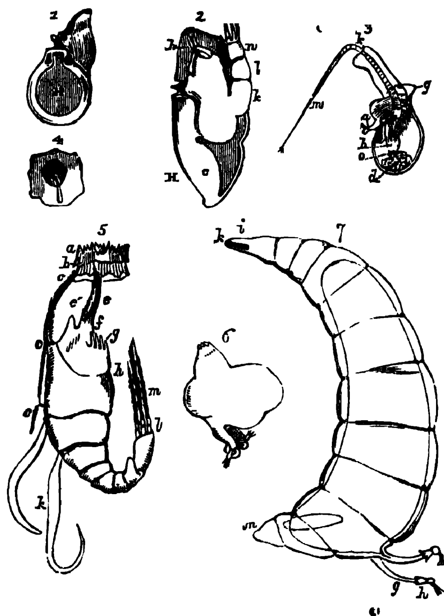


Fig. 69.—1. *Alcippe lampas*; female. 2. The same in sectional view. H. Horny disk of attachment; in 1, the males are visible as dark specks on either side of the upper part of the sac; *c*, ovary. *h*. First pair of cirri. *k*. *l*. *n*. Three segments of the thorax without cirri; the other three segments, bearing the three pairs of terminal cirri, are very short. 3. Male *Alcippe*. *a*. Antennary appendages. *b*. Vesicula seminalis. *o*. Eye. *d*. Testis. *k*. Orifice of the sac. *m*. Penis. 4. Burrow of *Alcippe* in a portion of a *Fusus* shell. 5. *Cryptophialus minutus* (female) with the outer integument removed. *e*. Labrum. *f*. Palpi. *g*. Outer maxillæ. *h*. Rudimentary maxillipede. *c*. Wall of sac continued above into the rim of the aperture *a*, *b*. *l*. *m*. Abdominal cirri. *k*. Appendages of unknown nature. 6. Male *Cryptophialus*. 7. *Proteolepas bivincta*. *m*. Mouth. *g*. *h*. Peduncle and antenna. *i*. *k*. Vesicula seminalis and penis. (After Darwin.)

tached by cement which covers the characteristic antennules

of a Cirripede. Within the sac is a thorax, with four pairs of rudimentary appendages terminated by a short abdomen. There is neither mouth, alimentary canal, nor gnathites, the cavity of the body being principally occupied by a great seminal vesicle; and no trace of female organs exists. This is, therefore, an accessory, or "complemental" male. In *Scalpellum ornatum*, the individuals are males and females, two of the former being lodged in cavities of the scuta of one of the latter, as in the preceding species, and in *S. rutilum*. The males have no mouth. *S. rostratum* has complemental males, provided with alimentary organs attached to the interior of the sac of the hermaphrodite, while *S. Peronii* and *villosum* have still more perfect complemental males fixed in a like position. In *Ibla Cumingii*, the female has a vermiform male, provided with well-developed alimentary organs, attached within her sac; but, in the only other species of this genus, *I. quadrivalvis*, a similarly constructed, but here only complemental male, is lodged in a relatively large hermaphrodite form.

With regard to the habits of the *Cirripedia*, the majority are merely cemented to foreign bodies. *Anelasma* and *Tubicinella*, however, partially bury themselves in the integuments of the shark and whale, and thus prepare us for the completely boring habit of *Cryptophialus*, *Lithotrya*, and *Alcippe*, the latter of which (Fig. 69, 1, 2, 3) burrows in dead shells on our own coasts.

Proteolepas lives within the sac of *Alepas cornuta*, and appears to be truly parasitic upon it, sucking the nutritive juices from the soft prosoma of the animal which it infests.

The *Cirripedia* are almost exclusively marine, only a few species tolerating even brackish water. The *Thoracica* alone have yet been found in the fossil state. The oldest known genus, *Pollicipes*, occurs in the lower oolite; there is a single cretaceous species of *Verruca*, but the sessile Cirripedes become numerous only in the tertiary epoch.

The RHIZOCEPHALA (*Peltogaster*, *Sacculina*) are small and parasitic; usually upon the abdomen of other *Crus-*

tacea (*Podophthalmia*). The body is like a sac or disk, and devoid of segmentation and of limbs. The aperture of the sac is funnel-shaped and supported by a ring of chitin. The circumference of the funnel gives off a number of root-like processes, which branch out through the body of the infested animal. The alimentary canal is obsolete, and there are no cement glands. They are hermaphrodite, and

Fig. 70.

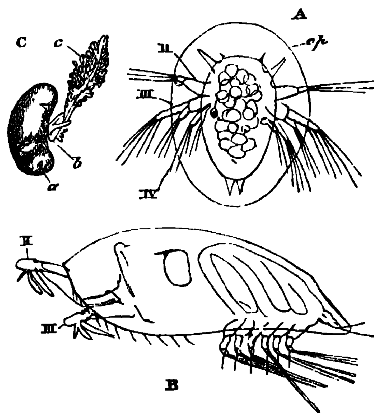


Fig. 70.—A. *Nauplius*-stage of *Sacculina purpurea* : *cp*, carapace. B. *Cypris*-stage of *Lernæodiscus porcellanæ*. C. Adult condition of *Peltogaster paguri* : *a*, anterior end of the body ; *b*, aperture ; *c*, root-like processes. (After F. Müller.)

the young, like those of the other *Pectostraca*, pass through a *Nauplius* and a *Cypris* stage.*

The Malacostraca.—The groups of *Crustacea* known as the *Podophthalmia*, the *Cumacea*, the *Edriophthalmia*, and the *Stomatopoda* are here included under this head.

* The term *Cypris*-stage, usually applied to that condition of the larvæ of the *Pectostraca* in which they are provided with a bivalve carapace, must not be taken to imply any special affinity with the *Ostracoda* On the contrary, the larva in the *Cypris*-stage is much more similar to a Copepod or Branchiopod.

The body consists of twenty somites (counting that which bears the eyes as one), and, of these, six (bearing the eyes, antennules, antennæ, mandibles, and two pairs of maxillæ) constitute the head; eight enter into the thorax, and bear the foot-jaws and ambulatory limbs; and six form the abdomen and swimming limbs. In some few instances the number of somites is reduced, but they never exceed twenty.

The *Nauplius*-form of the free embryo is rare, but occurs in some cases (*Peneus*). In others (*Mysis*) it is represented only by a temporary condition of the embryo, during which, however, a chitinous cuticula is formed and subsequently shed; and what appear to be remains of such a transitory record of an original *Nauplius* state, are seen in many *Amphipoda* and *Isopoda*, which nearly attain their adult form within the egg. In most *Podophthalmia*, the embryo leaves the egg, not as a *Nauplius*, but as a *Zoœa*, which has thoracic, but no abdominal, appendages, and in many respects resembles a Copepod.

The *Cumacea* take an intermediate position between the *Podophthalmia* and the *Edriophthalmia* on the one hand, and the *Phyllopoda* (*Nebalia*) on the other. They thus serve to connect the *Malacostraca* with the *Entomostraca*.

The PODOPHTHALMIA.—It will be convenient to commence the study of the *Malacostraca* with the *Podophthalmia*, and, as excellent examples of this division of convenient size are readily obtainable in the fresh-water Crayfish (*Astacus fluviatilis*) and the Lobster (*Homarus vulgaris*), and as they furnish a very intelligible guide to the general plan of structure of the higher *Arthropoda*, the organisation of *Astacus* will be described at length. With some unimportant modifications, what is said about it will be found to apply to the Lobster.

The upper and anterior portion of the dense and more or less calcified exoskeleton, which covers the body of *Astacus*, has the form of a large expanded, shield-like plate, the carapace, produced into a strong frontal spine be-

tween the eyes, and bent down at the sides, so as to reach the bases of the legs. The posterior division of the body, on the other hand, presents a very different aspect, being divided into a series of distinct moveable somites. This is called the abdomen, while the anterior division, covered by the carapace, corresponds with the head and thorax of other *Arthropoda*, and receives the name of cephalo-thorax.

On turning to the ventral surface of the Crayfish, a great number of limbs or appendages, twenty pairs in all, are seen to be attached to the cephalo-thorax and abdomen, six pairs belonging to the latter, and fourteen pairs to the former region of the body.

The six pairs of abdominal appendages are commonly known as the "false" or "swimming" feet; and it will be observed that they are attached to the six anterior segments of the abdomen only, the seventh being unprovided with any such organs. Of the fourteen pairs of cephalo-thoracic appendages, the five posterior are called the "ambulatory" legs, being the organs by which the Crayfish is enabled to walk. Strictly speaking, however, the anterior of the five pairs is not more ambulatory than prehensile, being so modified as to constitute the great claws or "chelæ."

Of the six next pairs of appendages, passing from behind forwards, five are not at first sight apparent, the posterior pair, which are applied over the mouth and cover the others, being alone visible. These and the two pairs which lie immediately under, or in front of them, are called *maxillipedes*, or "foot-jaws." The next two pairs, delicate and foliaceous, are the maxillæ; while beneath or rather in front of them, are two strong, toothed organs, the mandibles. These, the maxillæ and the maxillipedes, thus constitute six pairs of gnathites.

The remaining three pairs of appendages occupy the sides of the fore-part of the cephalo-thorax, in front of the mouth. The most posterior pair, or the long feelers, are the antennæ; the next, or the short feelers, are the anten-

nulæ; while the most anterior pair are the moveable stalks, which support the eyes upon their extremities; the "ophthalmic peduncles," or "ophthalmites."

To arrive at an understanding of the composition of this complex body, with its multiform appendages, we must first detach and study carefully one of the abdominal segments—say the third. Such a segment is nearly semicircular in vertical section, the dorsal wall, or tergum, being very convex, and where it reaches the level of the almost straight ventral wall, or sternum, sending down a flattened lobe, which is reflected at its free edges into a corresponding prolongation of the ventral wall, so that each infero-lateral angle of the segment is prolonged into a hollow process, the pleuron. Near the outer extremities of the straight ventral portion of the segment two rounded articular cavities, which receive the basal joints of the appendages, are situated. A transverse groove will be seen on the tergum, separating rather more than the anterior third of its surface, as a smooth, convex, lenticular facet, which is completely overlapped by the posterior margin of the preceding segment, when the abdomen is extended, and is left uncovered only in complete flexion. This is the *tergal facet*. A corresponding flattened and rather excavated surface upon the anterior half of the pleuron, which is similarly overlapped by the preceding pleuron, and is left uncovered only in complete extension, may be termed the *pleural facet*. It will be observed that there is a close correspondence between the skeleton of an abdominal somite of a Cray-fish, and that of a thoracic somite of a Trilobite; except that, in the latter, the sternal region is not calcified.

The appendages of the segment (Fig. 71, K) are very simple, consisting of a cylindrical basal portion, divided into two joints, a shorter proximal, and a longer distal, to the latter of which two terminal many-jointed filaments are articulated. The inner of these is distinguished from the outer by possessing a more elongated and wider basal joint. The whole basal division of the appendages is the

Fig. 71.

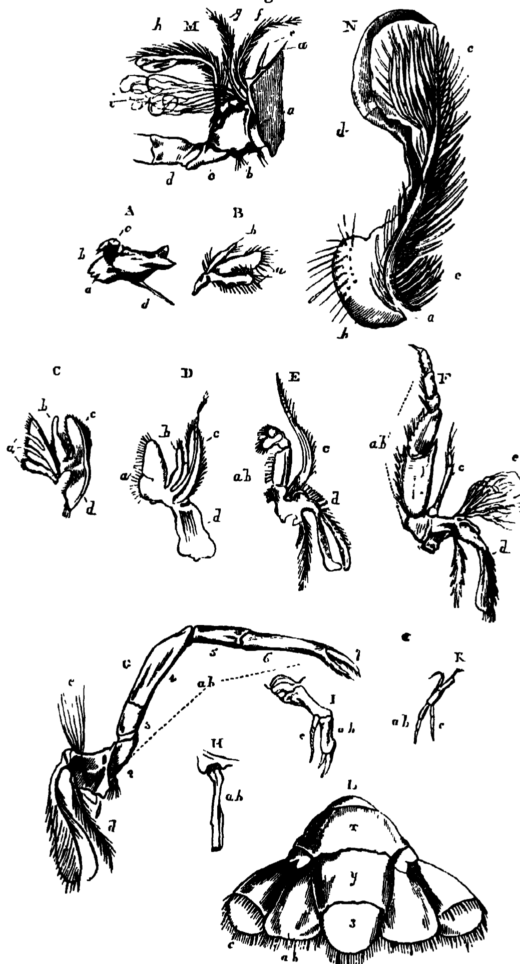


Fig. 71.—*Astacus fluviatilis.* A. Mandible. *a*, *b*, endopodite; *o*, its terminal joints constituting the palpus of the mandible. B. First maxilla. C. Second maxilla. D. First maxillipede. E. Second maxillipede. F. Third maxillipede. All the preceding, except B, are left limbs. G. Ambulatory leg. H. Appendage of first, and I, of second abdominal somite in the male. K. Appendage of third abdominal somite. L. Sixth abdominal somite, with its appendages and telson. *a*, *b*. Endopodite. *c* Exopodite. *d*. Epipodite. *e*. Setaceous filaments attached to coxopodite. *x*. Tergum of sixth abdominal somite. *y*, *z*. The two divisions of the telson. In G: 2, basipodite; 3, ischiopodite; 4, meropodite; 5, carpopodite; 6, propodite; 7, dactylopodite. In A. *d* marks the tendon of the adductor muscle, and, in K, the joints of *a b*, and *c* are not sufficiently numerous. M. Transverse section of half a thoracic somite (*a*). *b*. Coxopodite. *c*. Basipodite. *d*. Ischiopodite. *h*. Branchiferous epipodite. *f*, *g*. Branchiæ. *e*. Filiform appendage. N. One of the branchiferous epipodites. *a*. Its point of attachment. *b*. Basal enlargement. *c*. Branchial filaments. *d*. Terminal lobes.

protopodite; while the internal and external terminal filaments are the *endopodite* (*a b*) and *exopodite* (*c*).

An abdominal segment, or somite, then, is composed of a tergum, two pleura, and a sternum; but it must be remembered that these terms rather indicate regions than anatomical elements, the whole segment being continuously calcified, and no sutures or other absolute demarcations separating one portion from another. Furthermore, the somite carries two appendages, each divided into a proximal portion or protopodite, terminated by two branches, the endopodite and exopodite.

The whole exoskeleton of the *Astacus*, however various may be the appearance of its different parts, consists of somites and appendages essentially similar to those which have just been described, but which are more or less masked by the connation, the coalescence, the abortion, or the extreme modification of their primitive elements.

If, in the first place, we follow out these modifications in the posterior somites, we find the fourth, fifth, and sixth abdominal somites to be, in all essential respects, similar to the third; but the appendages of the sixth (Fig. 71, L) are singularly changed, the protopodite being represented by a single strong, short joint, and the exopodite and endopodite having the form of wide oval setose plates. The exopodite is again divided into two portions by a

transverse joint. The seventh division of the abdomen (Fig. 71, L, *y*, *z*) is the *telson*. This telson bears no appendages; dorsally it is completely calcified, but is divided by a transverse suture into two portions, the posterior of which is moveable upon the other; ventrally, on the contrary, it is only the posterior part which is fully calcified, the middle of the anterior portion, in which the anus is situated, being completely membranous, and the sides only being strengthened by calcareous plates extending inwards from the dorsal hard skeletal element, or *sclerodermite*.

The powerful tail-fin of the *Astacus* is formed by the telson, combined with the two distal divisions of the sixth abdominal appendages on each side. The other abdominal appendages can have very little influence on locomotion. In the female, however, they play an important part, as the carriers of the eggs; and, in this sex, there is nothing worthy of special notice about the first and second abdominal somites or their appendages, except that those of the first are rudimentary. In the male, the appendages of these two somites have undergone a very interesting metamorphosis, whereby they are fitted to subserve copulation. Those of the second somite (Fig. 71, I) are enlarged, and the protopodite and basal joint of the endopodite are much elongated; the latter being produced internally into a plate rolled upon itself, and thence concave outwards and forwards. It is as long as the rest of the endopodite (which like the exopodite is many-jointed) and serves as a sort of sheath for the reception of the appendage of the first abdominal somite (Fig. 71, H) which consists of a single plate rolled upon itself in a similar manner, so as to resemble a grooved style. These organs, doubtless, help to convey the spermatophores from the male genital apertures to the body of the female.

The compact and firm cephalo-thorax seems at first to differ widely from the flexible, many-jointed abdomen; but the most posterior of its somites offers an interesting transition from the one to the other. This somite is, in fact, only united by membrane to that which precedes it, and is hence,

to a certain extent, moveable. Its sternal portion is completely calcified, but the *epimera* * are only partially calcified.

The appendages of this somite differ widely from those of the abdomen, representing (as their development shows) only the protopodite and endopodite of the latter. Each is a long firm leg, composed of seven joints, the proximal one being thicker than any of the rest, while the terminal joint is narrow, curved and pointed. To these seven joints, Milne-Edwards has applied the following terms (Fig. 71, G). The proximal one which articulates with the somite, is the *coxopodite* (1), the next, small and conical, is the *basipodite* (2), the third cylindrical, short, and marked by an annular constriction, is the *ischiopodite* (3). Next comes a long joint, the *meropodite* (4), then the *carpopodite* (5) and *propodite* (6), and, finally, the terminal *dactylopodite* (7). †

The next four somites, proceeding anteriorly, have a similar general character to that which has just been described, but they cease to be moveable upon one another, partly by reason of the calcification of the interepimeral and intersternal membranes, partly on account of the development of these membranes by a folding inwards, or involution, into processes, the *apodemes*, which project inwards and unite with one another in the cavity of the thorax. In an *Astacus* which has been macerated, or, better, boiled in caustic alkali, the floor of the thoracic cavity is seen to be divided into a number of incomplete cells, or chambers, by these apodemal partitions, which will be observed, on careful examination, to arise partly from the intersternal, partly from the interepimeral membrane connecting every pair of somites. The former portion of each apodeme is the *endosternite*, the latter the *endopleurite* of Milne-Edwards. As a general rule, each endosternite is

* The term *epimeron* is here employed in a more special sense than that commonly used, to denote that part of the lateral wall of a somite which is situated between the articulation of the appendage and the pleuron.

† Probably the coxo- and basipodite together answer to the protopodite of the abdominal appendages, the remaining joints representing the endopodite.

distinguishable into three apophyses—the *arthrodial*, which passes outwards and unites with the descending division of the endopleurite to form one boundary of an articular cavity for a limb; the *mesophragmal*, which is directed inwards, uniting with its fellow, and forming an arch over the passage left in the middle line between each pair of endosternites—the so-called *sternal canal*; lastly, the *paraphragmal* division is a small process, which passes forwards, upwards, and outwards, and unites with the anterior division of its own endopleurite, and with the posterior division of the endopleurite in front of it.

The endopleurite, likewise, divides into three apophyses, one descending or arthrodial, and two which pass nearly horizontally inwards: the anterior horizontal apophysis uniting with its own paraphragmal apophysis, the posterior with the paraphragmal of the antecedent endosternite. The posterior horizontal apophysis, therefore, crosses the space between every pair of apodemes diagonally, whence the appearance of a double row of longitudinal cells opening above, on each side of the sternal canal. It will be understood, however, that these cells are very incomplete, communicating with one another anteriorly and posteriorly, by the large apertures left between the endosternites and endopleurites; and, laterally, by the spaces between the endosternites, through which each series opens into the sternal canal; while above, they are in free communication with the thoracic cavity. The apodemes give attachment to the muscles of the appendages, while the chain of ganglia and the sternal artery lie in the sternal canal.

The appendages of the penultimate, resemble those of the last, thoracic somite, but the three preceding pairs differ from them by being chelate, that is, by having the posterior distal angle of the propodite produced so as to equal the dactylopodite in length, and thus constitute a sort of opposable finger for it (Fig. 71, G, 6, 7). The first ambulatory or prehensile limb, again, is remarkable for its great size and strength, and for the ankylosis of its basipodite with the ischiopodite.

The four anterior pairs of ambulatory limbs differ from the last pair in possessing a long curved appendage (Fig. 71, N), which ascends from the coxopodite, with which it is articulated, and passes into the branchial chamber, in which it lies. This is the *epipodite;* its relation to the function of respiration will be adverted to presently.

The sterna, which are wide in the three hindmost thoracic somites, become very narrow and almost linear in the anterior ones. They and their apodemes, however, remain perfectly recognisable.

The sternal regions of the three maxillipedary somites have the same characters, their appendages and articular cavities becoming smaller; while, by the contemporaneous excessive narrowing of the interarticular regions of the sterna, these cavities are closely approximated.

The sternum of the next anterior somite (bearing the second pair of maxillæ), on the other hand, though very narrow from before backwards, has a considerable width, and its articular cavities, already much larger than those of the anterior maxillipedary somites, are consequently thrown outwards. Hence results a sudden widening of the second maxillary, as compared with the first maxillipedary somite; and, as a consequence, we find a deep fold or depression on the sides of the body, where these two somites join. This fold is directed upwards and backwards on the flanks of the body, parallel with an important impression on the carapace, the *cervical* groove. Not only on this ground, but because the fold really represents a true neck, or separation between the head and thorax, it may approximately be termed the *cervical fold.* The scaphognathite, (Fig. 71, C, *c, d,*) an important appendage of the second maxilla, lies in this cervical fold.

The appendages of the three maxillipedary somites (Fig. 71, D, E, F) are highly interesting, inasmuch as they afford transitional forms between the ambulatory limbs and the gnathites. Each maxillipede is composed of three divisions, articulated with a stout protopodite. The outermost of these divisions is a curved, elongated lamina

(*d*), precisely resembling the epipodite of the posterior thoracic limbs in the two hinder maxillipedes (E, F); but, in the anterior (D) not modified so as to serve as a branchia, and rather approaching the scaphognathite in form.

The middle division of each maxillipede (*c*), answering to the exopodite, is long, slender, many-jointed, and palpiform, while the inner division, or endopodite, (*a*, *b*,) not only corresponds with one of the ambulatory limbs, but in the posterior maxillipede (Fig. 71, F) very closely resembles one, and contains the same number of joints. In the next maxillipede, however (Fig. 71, E), the endopodite is proportionally shorter, and in texture and form rather approaches the foliaceous endopodite of the anterior maxillipede (Fig. 71, D), in which a flat plate is applied to the posterior surface of the slender exopodite. A perfect transition is thus produced between the corresponding divisions of the second maxillipede and of the second maxilla.

The intermaxillary apodeme, or that developed from the connecting membrane of the two maxillary somites, is very remarkable for its stoutness and for the great size and expanded form of the mesophragmal processes, which unite into a broad plate, whence prolongations are sent forwards and outwards, in front of the tendon of the great *adductor mandibulæ* muscle on each side. These prolongations appear to be the calcified posterior horizontal apophyses of the mandibulo-maxillary apodeme, which elsewhere remains membranous.

The second maxilla (Fig. 71, C) much resembles the anterior maxillipede, but the epipodite (*d*) and exopodite (*c*) appear to be combined into a wide oval plate, the *scaphognathite,* of which mention has already been made.* In the first maxilla (Fig. 71, B) the epipodite and exopodite appear to be undeveloped, and the joints of the endopodite are completely foliaceous. The somite which supports the

* Until the development of these appendages has been worked out, the determination of the homologies of their parts must be regarded as provisional.

mandibles is, to a great extent, membranous in its sternal region; it is united with the corresponding region of the first maxillary somite, itself represented merely by a narrow, distinctly calcified, band, in front of the second maxillary sternum, by membrane only. In this membranous space the elongated aperture of the mouth is situated.

On each side of, and behind, the mouth are two little elongated oval calcified plates, between which, an oval process, setose at its extremity, proceeds downwards and forwards, and lies in close apposition with the posterior face of the mandible of its side. This is one-half of what is termed by most authors the *labium*, but, to avoid confusion with the labium of *Insecta*, from which it is wholly different, it may be called the *metastoma* (Fig. 72, *f*). It obviously answers to the structure so named in the *Copepoda*.

The mandibles fill up a large space in the sternal membrane, with which their edges are continuous on each side of the oral aperture; externally, the sternal membrane bends suddenly downwards into the pleural ridge, continuous with the branchiostegite of the carapace, and becomes calcified; while, anteriorly, it is very difficult to say where the mandibular sternum terminates. In front of the mouth the sternal membrane becomes developed into a large median lobe, containing three small calcified plates on each side of the middle line. This is the labrum (Fig. 72, *e*).

The mandible itself (Fig. 71, A) is thick and strong at its inner end, where it is divided by a deep excavation into an upper and a lower portion, (*a*, *b*,) the edge of each being toothed. The outer division of the mandible extends along the whole width of the somite, and tapers to its extremity, which presents an articular head, the outer condyle. Attached to its anterior margin is the palp (*o*), which represents the terminal joints of the mandibular endopodite. The exopodite and the epipodite have no representatives in this appendage. Superiorly, the outer portion of the mandible is concave, and its posterior edge

gives attachment to the calcified tendon of the adductor mandibulæ (d).

In front of the labrum and mandibles is a wide, somewhat pentagonal area, prolonged into a point in the middle line forwards, and presenting a small' spine on each side; this is the *epistoma* (Fig. 72, B, l), and it is chiefly, if not entirely, formed by the sternum of the antennary somite. On each side of its triangular anterior extremity it pre-

Fig. 72.

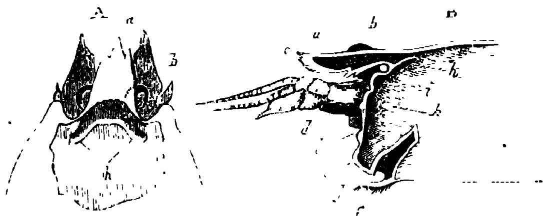


Fig. 72.—A. Anterior extremity of the cephalo-thorax of *Astacus*, with a portion of the carapace removed. B. Vertical section of the anterior part of the cephalo-thorax. a, rostrum; b, ophthalmic peduncles; c, antennulæ; d, antennæ; e, labrum; f, metastoma; g, oral aperture; h, procephalic processes; i, ophthalmic sternum; k, antennulary sternum; l, antennary sternum or epistoma.

sents a wide articular cavity for the articulation of the antennæ. In these organs (Fig. 72, B, d) the same parts can be recognised as in the other appendages, viz., an imperfect basal joint, produced into a prominent cone, perforated behind and internal to, its apex; and here called *coxocerite*. Next, a *basicerite*, to the outer portion of which a flattened plate, the representative of the *exopodite*, and here called the *scaphocerite*, is articulated; while to its inner portion an *ischiocerite* is connected, bearing a *merocerite* and *carpocerite*, while the last segment, or *procerite*, consists of a long multi-articulate filament.

The sterna of the next two somites are narrow and elongated; that of the antennary somite is well calcified, but that of the ophthalmic somite is almost entirely membranous.

The antennules (Fig. 72, B, *c*) present an enlarged trigonal basal joint, succeeded by two others. These represent the protopodite, and carry at their extremities two many-jointed filaments, which probably represent the exo- and endopodites.

The peduncles of the eyes (Fig. 72, *b*), lastly, are composed of two joints, a small proximal *basiophthalmite*, and a larger terminal *podophthalmite*.

Such are the structure and arrangement of the sternal portions of the several cephalo-thoracic somites, and the nature of their appendages. On regarding the sternal region as a whole, there are yet some very important points (the morphological value of which has been fully pointed out by Milne-Edwards) to be noticed. A longitudinal median section, in fact, shows, that while a line drawn through the sterna of the somites behind the mouth is nearly straight and parallel with the axis of the body, a similar line drawn through the sterna of the somites, in front of the mouth, ascends as it passes through the antennary, antennulary and ophthalmic sterna, and thus takes a position at right angles to the former line (Fig. 72, B). The sterna of the somites, in front of the mouth, are, therefore, bent up so as to look forwards instead of downwards; and it is of essential importance to bear in mind this *cephalic flexure*, in considering the structure of the head in these and other *Arthropoda*.

Just as the lateral regions of the abdominal somites are produced into the *pleura*, so are the lateral regions of the cephalo-thorax similarly prolonged. Thus the membranous lateral walls of the posterior cephalo-thoracic somite are reflected superiorly, and bent down again to the level of the bases of the legs, where they become continuous with a calcified layer corresponding with the tergal half of the pleura, and forming the posterior part of the carapace. In like manner, the more or less calcified epimera of all the other somites are reflected superiorly into a membrane which passes downwards, and the free lower edge of which is continuous with the edges of the carapace. The carapace,

therefore, corresponds in position with the terga and tergal halves of the pleura of all the somites which are thus reflected into it, and these somites include all, without exception, from the last thoracic to the ophthalmic. Posteriorly, the edges of the carapace are a little prolonged beyond the last thoracic somite, and take the form of a fold, with an under layer distinct from the upper. Anteriorly, in the middle line, the carapace is prolonged in a similar manner, but to a much greater extent; it thus gives rise to the long *rostrum*, which overhangs the sterna of the ophthalmic and antennulary somites. At the sides of the antennulary and antennary somites the rostral prolongation of the carapace is the direct continuation outwards of the epimera of those somites, and there is nothing to be compared to an apodeme; but the sternum of the ophthalmic somite, after giving off the lamella which forms the inferomedian region of the rostrum, is prolonged on each side of the middle line backwards and outwards into a free, expanded, thin, calcified process, which applies itself against the carapace by its upper surface, and by its under surface gives attachment to the anterior gastric muscles. Corresponding processes are developed from the carapace itself, in some *Podophthalmia* (e. g. *Galathea*, *Carcinus*), for the attachment of the posterior gastric muscles. From the last thoracic to the maxillipedary somites, the pleural, or free part of the carapace, termed, from its function, the *branchiostegite*, or cover of the gills, encloses a wide space, bounded internally by the epimera of the somites. This is the *branchial chamber*. In front of the maxillipedes and cervical fold, however, the chamber suddenly becomes narrowed by the rapid widening of the sterna of the maxillary and mandibular somites, and by the lowering of the point at which the reflection of their epimera into their pleura takes place. Finally, on the antennary somite, and in front of it, the pleuron becomes a mere fold separated by a shallow groove, the representative of the branchial chamber, from the epimera.

On the dorsal surface, there is no indication of any division

of the carapace into terga corresponding with the sterna of the somites, but it is marked by a well-defined, curved groove, the posterior convexity of which extends across the carapace, rather behind its middle, and the lateral portion of which runs downwards and forwards, towards the anterior part of the antennary sternum. This is the *cervical groove;* that part of the carapace which lies in front of it is the *cephalostegite,* while that which is behind is the *omostegite.*

The omostegite, again, is divided into three portions by a groove on each side of the middle line—the *branchio-cardiac* grooves. The branchiocardiac groove, and the lateral portion of the cervical groove, on the dorsum of the carapace, correspond very closely with the line at which the epimeral is reflected into the pleural membrane, on its ventral surface. The transverse portion of the cervical groove, on the other hand, corresponds with the posterior boundary of the stomach, and the anterior extremity of the heart, and continues inwards the line of the cervical fold; so that, in a longitudinal section of an *Astacus,* the direction of the cervical fold, if followed upwards and backwards, strikes against the inner surface of the carapace, at a point corresponding with the summit of the cervical groove, on its outer surface. By cutting through the cervical fold, therefore; through the membrane joining the second maxillary with the first maxillipedary sternum; and through the carapace in the transverse part of the cervical groove, it is possible to separate an anterior portion of the cephalo-thorax, containing the whole of the cephalostegite, and the first six somites, with their appendages, from a posterior portion, consisting of the omostegite, and the last eight cephalo-thoracic somites. And, in making this artificial separation, we should be merely carrying out a distinction between these two sets of somites, already very clearly indicated by the cervical fold and groove.

It is for this reason that I differ from Milne-Edwards in regarding the somite which bears the first maxillipedes as the first of the thorax, and not as the last of the head. And the acceptance of this natural delimitation of the

head in the higher *Crustacea*, has the advantage of bringing its structure into accordance with that of the same region in the *Entomostraca*, in which it is the rule that the head possesses eyes, antennules, antennæ, mandibles, and two pairs of maxillæ.

Another mark upon the carapace is a large and rounded convexity, occupying nearly a third of the whole width of the posterior half of the cephalostegite. This impression is bounded internally by a line drawn from the outer angle of the base of the rostrum, directly backwards; and, externally by a curved depression, deepening into a pit anteriorly; it corresponds with the attachment of the base of the adductor muscle of the mandible.

The mouth of the Crayfish is a wide aperture, situated between the labrum in front, the metastoma behind, and the mandibles on each side. It serves as the entrance to an equally wide œsophagus, a short tube with plaited walls, which takes a slightly curved direction upwards and a little backwards, to open into the large stomach, which is not only situated directly over, but extends forwards in front of, the gullet. The stomach, in fact, occupies almost the whole cavity of the body in front of the cervical suture, and is divided by a constriction into a large anterior moiety, the cardiac division, and a small posterior, pyloric portion. The anterior half of the cardiac division has the form of a large membranous bag, the inner surface of which is closely set with minute hairs; but, in the posterior half of this, and on the whole of the pyloric division, the walls of the stomach are strengthened by a very peculiar arrangement of uncalcified and calcified plates and bars articulated together, which are thickenings of the chitinous cuticula of the epithelium of the alimentary canal, and constitute the gastric skeleton. The most important part of this apparatus is that which is developed in the posterior cardiac region.

It consists, in the first place, of a transverse, slightly arcuated *cardiac* plate (Fig. 73, *ca*), calcified posteriorly, which extends across the whole width of the stomach, and

articulates at each extremity by an oblique suture with a small curved triangular *antero-lateral* or *pterocardiac* (*pt*) ossicle. On each side, a large, elongated *postero-lateral* or *zygocardiac* ossicle (*se*) wider posteriorly than anteriorly, is connected with the lower end of the antero-lateral ossicle, and, passing upwards and backwards, becomes continuous with a transverse arcuated plate, calcified in its anterior moiety, and situated in the roof of the anterior dilatation of the pyloric portion; this is the *pyloric* ossicle (Fig. 73, *py*).

These pieces, it will be observed, form a sort of six-sided frame, the anterior and lateral angles of which are formed by moveable joints, while the posterior angles are united by the elastic pyloric plate.

From the middle of the cardiac piece a strong calcified *urocardiac* process (*ca'*) extends backwards and downwards, and, immediately under the anterior half of the pyloric ossicle, terminates in a broad, thickened extremity, which presents inferiorly two strong rounded tuberosities, or *cardiac* teeth. With this process is articulated, posteriorly, a broad *pre-pyloric* ossicle, which passes obliquely upwards and forwards, in the front wall of the anterior dilatation of the pyloric portion, and articulates with the anterior edge of the pyloric ossicle, thus forming a kind of elastic diagonal brace between the urocardiac process (*ca'*), and the pyloric ossicle. The inferior end of this pre-pyloric ossicle is produced downwards into a strong bifid *urocardiac* tooth (*ac*). Finally, the inner edges of the postero-lateral ossicles are flanged inwards horizontally, and, becoming greatly thickened and ridged, form the large *lateral cardiac* teeth (*cc*). The membrane of the stomach is continued from the edges of the pre-pyloric to those of the postero-lateral ossicle in such a manner as to form a kind of pouch with elastic sides, which act, to a certain extent, as a spring, tending to approximate the inferior face of the pre-pyloric ossicle to the superior face of the median process of the cardiac ossicle.

The result is that there is a certain position of equilibrium

of the whole apparatus, when the urocardiac process and the pre-pyloric ossicle make a small angle with one another,

Fig. 73

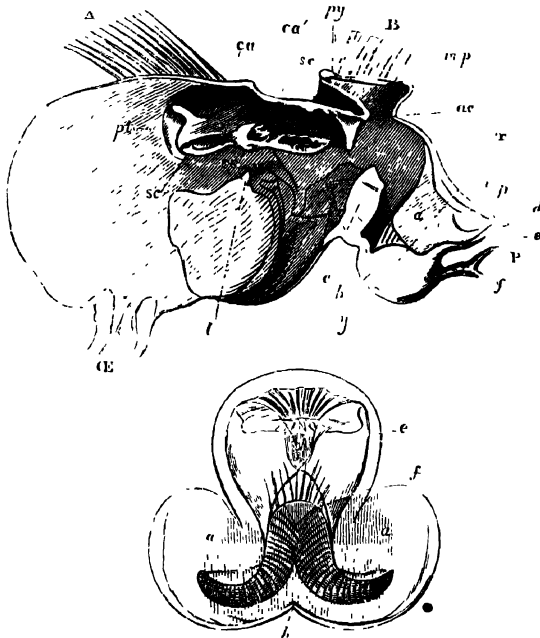


Fig. 73.—*Astacus.*—Upper Figure: Longitudinal Section of Stomach. A. Anterior gastric muscle. B. Posterior gastric muscle. Œ. œsophagus. P. Pylorus. *ca.* Cardiac ossicle. *c a'.* Its urocardiac process. *a c.* Urocardiac tooth. *py.* Pyloric ossicle. The oblique bar, extending from the end of the cardiac to the pyloric, is the prepyloric ossicle. *pt*, pterocardiac. *s e.* Postero-lateral cardiac, with its great tooth, *c c.* *l.* Small inferior tooth. *c* Cardio-pyloric valve. *b.* Infero-median pyloric ridge. *a.* Lateral pyloric ridge. *d.* Superior pyloric ridge. *u p.* Uro-pyloric ossicle. *x y.* Line of section; the anterior face of the posterior segment being shown in the lower figure.

and the antero-lateral ossicles form an almost unbroken transverse curve with the cardiac. When undisturbed, the apparatus tends to assume this position.

Two pairs of powerful muscles are attached to this gastric skeleton. The anterior pair arise from the procephalic processes, and are inserted into the roof of the stomach, somewhat in front of the cardiac ossicle; the posterior have their origin in the carapace immediately above and behind the pyloric end of the stomach, and their insertion into the pyloric ossicle and the wide posterior part of the postero-lateral pieces.

From the attachment of these muscles it is clear that their action must, in a general way, resemble that produced by pulling upon the cardiac and pyloric pieces when the stomach is removed from the body. Now the result of doing this is that, the cardiac and pyloric pieces being divaricated, the pre-pyloric ossicle assumes a vertical position, and the uro-cardiac tooth turns downwards and forwards. At the same time the antero-lateral or pterocardiac pieces are pulled backwards, and, owing to their oblique articulation with the cardiac piece, their inferior ends move downwards, backwards, and inwards, carrying with them the anterior ends of the postero-lateral pieces, the teeth of which (lateral cardiac) come into contact with the uro-cardiac and cardiac teeth, with a force proportional to that exerted in traction. On ceasing to pull, the apparatus returns to its former position, its backward movement being facilitated by the reaction of the elastic pouch mentioned above, and being doubtless also assisted, in the living state, by a pair of small *cardio-pyloric* muscles, which pass, one on each side, between the cardiac and pyloric ossicles, beneath the membrane of the stomach, the looseness of which, in this region, where it unites the various ossicles of the gastric mill, greatly assists the free movement of the whole apparatus.

Nothing can be more easy than to perform the experiment, and to convince oneself that these structures do really constitute a most efficient masticatory apparatus; and it is surprising that Oesterlen, in his elaborate essay on the stomach of *Astacus*, should have questioned the crushing action of the teeth.

A great bilobed valvular process (Fig. 73, *c*) rises up from the sternal region of the stomach, opposite the cardio-pyloric constriction, and apparently prevents the food from passing into the pyloric division until it is properly comminuted. And, in front of this valve, the infero-lateral parietes of the stomach are strengthened by a number of other plates and bars; one of which on each side bears a small tooth (*infero-lateral cardiac*, *l*), and is continued into a broad uncalcified plate, lying in the hinder and lower part of the side walls of the stomach, and covered with hairs internally. There are, therefore, altogether seven gastric teeth, three median, the cardiac, and the uro-cardiac; and two lateral on each side, the lateral cardiac, and the infero-lateral cardiac.

In the pyloric division of the stomach the food has to undergo a further series of comminutions and strainings. A ridge covered with long hairs projects in the median line above; other hairy ridges extend inwards from the sides to meet it, and nearly close the passage laterally. These ridges are very convex inferiorly, and their convexities abut against the concavities of an inferior median ridge, which rises up to meet them, and is prolonged posteriorly into a sort of valvular process, covered at its termination with long hairs, which bar the space left between the upper parts of the lateral ridges. The concave faces of this median process are covered by close-set parallel ridges, which only become free hair-like processes at the posterior margin of the plate, each ridge giving attachment to a regular series of minute hairs. These are directed inwards nearly parallel with the surface, which looks at first as if it were merely ruled with close-set transverse lines, connected by still finer and closer longitudinal ones.

This apparatus constitutes the "ampoule cartilagineux" of Milne-Edwards. Behind it there is yet another infero-median, and two lateral setose, valvular prominences, which form the last barrier between the food and the intestine.

Mr. T. J. Parker, who has recently carefully examined the

structure of the stomach of the Crayfish,* finds that, besides the anterior and posterior gastric and the cardio-pyloric muscles, there are intrinsic fibres in the walls of the stomach, some encircling the posterior pyloric region, others passing between the hindermost accessory ossicle and the postero-lateral and pyloric pieces; these must tend to diminish the cavity of the stomach, and the last-named fibres possibly assist in mastication by bringing the lateral cardiac into contact with the infero-lateral cardiac tooth. Moreover there are nine pairs of minor extrinsic muscles, of which two pairs pass from the anterior wall of the stomach and gullet to the antennary sternum, passing between the œsophageal commissures and on either side of the azygos nerve of the visceral system; three pairs pass between the side walls of the stomach and œsophagus and the mandibular sterna; a sixth pair arises from the forward processes of the intermaxillary apodeme and is inserted into the œsophagus; two more pairs arise, one from the internal thickened edge of the mandible, the other from the intermaxillary apodeme, and are inserted into the inferior surface of the pyloric region; and a ninth pair arises from the carapace just behind the posterior gastric muscles, and goes to be inserted into the posterior pyloric dilatation. There are also a few more inconspicuous fibres passing between the œsophagus and the neighbouring hard parts. All these, at least when acting together, must antagonise the intrinsic muscles, and dilate the stomach.

The pyloric portion of the stomach passes into the anterior portion of the intestine, which is smooth internally, and presents superiorly a cæcal process, the remains, according to Rathke, of one lobe of the vitellary sac of the embryo.

This anterior portion of the intestine is, however, very short, and almost immediately becomes dilated into the wider posterior division, which extends to the anus. The inner surface of the dilatation is produced into six ridges, which are continued into a corresponding number of series of papillæ along the rest of the intestine.

The only glandular apparatus of any kind which opens

* 'Journal of Anatomy and Physiology,' Oct. 1876.

into the alimentary canal is the liver, and the apertures of the wide hepatic ducts are seen on each side of the pylorus. Each duct conveys the secretion from the multitudinous cæcal tubes, which constitute the principal mass of the corresponding bilobed half of the liver. The two halves lie on each side of the stomach, and, though they remain perfectly distinct from one another, come into close contact below.

Astacus possesses neither salivary glands nor any cæcal appendages to the intestine, such as exist in the *Brachyura* and some *Macrura*, unless the short cæcum just now described is the homologue of the longer cæca of *Maia* and *Homarus*.

In the spring and summer, two very curious discoidal calcareous plates, the so-called "eyes" of the Crayfish, are found imbedded in the walls of the dilated anterior portion of the cardiac division of the stomach, the middle of the lateral surface of which they occupy. These bodies commence as calcareous deposits underneath the chitinous gastric lining, and increase in size until the period arrives at which the Crayfish casts its skin. They are then cast, together with this lining membrane and the gastric armature; and it would appear that, like the latter, they become broken up and destroyed within the new stomach. The purpose of these concretions is not understood; the ordinary theory, that they are stores of calcareous matter, ready to be distributed through the young integument after ecdysis, appearing to be negatived by their small size. Oesterlen states that they rarely weigh more than two grains, and judiciously suggests, that if it be admitted that the Crayfish can derive all the calcareous matter it requires, except two grains, from other sources, it is hardly necessary to look on those two grains as a special supply.

The circulatory apparatus of *Astacus* is well developed. The heart (Fig. 74, C) has the shape of an irregular polygon, and lies immediately behind the stomach and beneath the cardiac region of the carapace, in a chamber which is commonly termed the "pericardium," to the walls of which

Fig. 74.

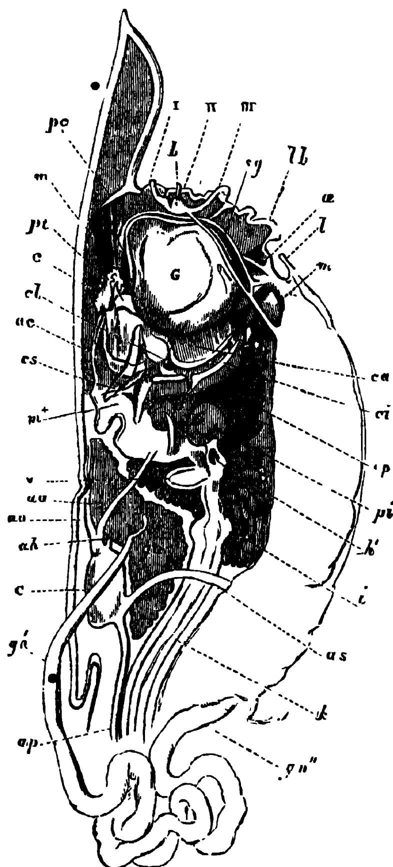


Fig. 74.—*Astacus*, Longitudinal Section.—I. II. III. Sterna of first, second, and third somites. *æ*. Œsophagus. *lb*. Labrum. *l*. Metastoma. G. Membranous part of the stomach. *c*. Cardiac ossicle. *p t*. Pterocardiac. *u c*. Urocardiac. *c l*. Lateral cardiac. *p*. Cardio-pyloric valve. *p i*. Inferior pyloric valvular apparatus. *m*. Anterior gastric muscle. *m**. Insertion of posterior gastric muscles. *p c*. Procephalic processes. *h'*. Opening of hepatic duct. *v*. Pyloric

cæcum. *i, k.* Intestine. *g n.* Testis. *g n'. g n''.* Vas deferens. C. Heart. *a o.* Ophthalmic artery. *a a.* Antennary. *a h.* Hepatic. *a s.* Sternal. *a p.* Superior abdominal artery. *b.* Cerebral ganglia. *s g.* Azygos visceral nerve.

it is attached by six ligaments, corresponding with the alæ of the heart in insects, but not, like them, muscular. Except by these ligaments, and by the arteries, which pass through it, the walls of the pericardial cavity, or blood sinus (for such it really is), are wholly unconnected with the heart, which thus is, in a manner, suspended freely in the blood.

Six apertures, two of which are superior, two inferior, and two lateral, provided with valves, which open inwards, allow the blood to enter the cavity of the heart during the diastole, and prevent its egress, except by the arteries, during the systole. The arterial trunks are six in number, five being given off anteriorly, and the other from the posterior portion of the heart.

Of the five anterior arteries one, the ophthalmic, is single, and situated in the middle line; it passes forwards on the stomach to the head, where it supplies the eyes and antennules. The other arteries are in pairs; two pass on the stomach forwards and outwards, giving off branches to the carapace, and eventually supplying the antennæ; the other two pass downwards, between the anterior lobes of the genitalia, and divide into a multitude of branches upon the hepatic cæca.

The posterior trunk, or sternal artery, is the largest of all, and presents a sort of bulbus arteriosus at its commencement. It turns almost directly downwards, usually on the right side of the intestine, to the sternal canal, which it enters, passing between the antepenultimate and penultimate thoracic ganglia to the lower surface of the ganglionic cord; it gives off two abdominal branches, one superior, close to its origin from the heart, which traverses the middle of the tergal region above the intestine, the other inferior, which takes a corresponding course along its sternal region beneath the nervous system. The arterial trunks are provided with valves at their commencement, so arranged as to prevent the regurgitation

of the blood. They ramify minutely, but how far a capillary system can be said to exist, is a question requiring further investigation. In transparent *Zoeæ*, I have plainly observed the abrupt termination of the arterial trunks by open mouths, through which the blood was poured into wall-less lacunæ, and into the general cavity of the body; nor can there be the least doubt that a similarly lacunar condition of the circulation exists in those lower adult *Crustacea*, the transparency of which allows of their examination with the requisite powers of the microscope. The probability is that a similar state of things obtains in the vascular system of all other *Crustacea*, and that, after undergoing a greater or less amount of subdivision, the arterial vessels, or their capillary continuations, cease to exist, the blood then making its way into lacunæ between the organs, and into the general perivisceral cavity; and, as in most *Mollusca*, ceasing to be contained in vessels with distinct walls.

The blood thus poured out, eventually makes its way into irregular sinuses or reservoirs, the chief of which, lodged in the sternal canal, communicates by lateral channels with others which lie above the bases of the thoracic appendages, and from which the afferent branchial canals pass into the stems of the branchiæ, on the exterior faces of which they ascend, giving off branches to the lateral filaments. Corresponding canals return the blood from these filaments to the efferent branchial canals, which run down the inner side of the branchial stems, and unite above the bases of the limbs into six trunks, which ascend beneath the epimera and open into the sides of the pericardial sinus. The floor of this sinus is formed by a continuous membrane, which appears to shut it off completely from the general visceral cavity (at least it retains air or fluid thrown into it), and, if this be really the case, it may be said to be functionally a branchial auricle, containing pure unmixed aerated blood.

The branchiæ are eighteen in number upon each side, and are attached from the eighth to the fourteenth somites inclusively. Six of these branchiæ are attached to the

epipodites of the eighth to the thirteenth somites, and differ very considerably in appearance from the other twelve. Each epipodite is, in fact, expanded at its upper extremity into a broad, bilobed membrane, which is folded upon itself, so that the two lobes are directed posteriorly, and receive the epipodite of the next limb (Fig. 71, N). The membrane of the lobes is obliquely plaited, so that, doubtless, they subserve respiration to a certain extent; but, in addition, the anterior edge of the epipodite is beset with a number of branchial filaments, similar to those on the other branchiæ.

The latter (Fig. 71, M, *f*, *g*) are simple plumes, consisting of a stem, to which are attached many delicate, cylindrical filaments. Two of these plumes are attached to the epimera and coxo-epimeral articular membranes of the ninth, tenth, eleventh, twelfth and thirteenth somites. They increase in size posteriorly. The eighth and fourteenth somites, on the contrary, only carry one plume. A tuft of long byssus-like filaments is attached to the coxopodite of each of the last six thoracic appendages (Fig. 71, F, M).

The respiratory organs of the Crayfish, not being provided with cilia, require some special arrangement for the renewal of the water with which they are in contact. This object is attained principally by the action of the scaphognathite, which lies immediately behind the anterior opening of the branchial chamber; and, during life, is incessantly in motion, baling out, as it were, the water which has become impure through the anterior opening, and thus compelling the flow of fresh fluid into the branchial chamber through its posterior and inferior opening, constituted by the space left between the lower edge of the branchiostegite and the bases of the limbs.

The nervous system of *Astacus** is composed of thirteen principal ganglionic masses, of which one, cerebral, lies in the head, in front of the mouth; six, thoracic, are situated

* For the histology of the nervous system, see an elaborate essay by Haeckel, on the minute structure of the tissues of the Crayfish, in the 'Archiv für Anatomie,' 1857.

in the sternal canal; and six, abdominal, lie in the median sternal region of the six anterior somites of the abdomen.

The cerebral ganglia (Fig. 74, *b*; Fig. 75, *a*) give off nerves to the eyes and to the muscles of the ophthalmic appendages; to the antennules and the auditory organs which they contain; to the antennæ and the sac of the antennary gland; to the carapace in front of the cervical suture; and finally they send posteriorly two long and stout commissural cords to the anterior thoracic ganglionic mass. These commissures are connected by a transverse

Fig. 75.

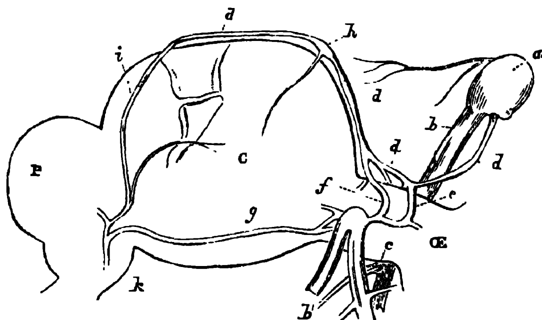


Fig. 75.—Visceral nerves of *Astacus*.—*a*. Cerebral ganglia. *b*. Commissures, that of the right side is cut and turned back. *c*. Transverse cord uniting them behind the œsophagus, Œ. *d*, *d*, *d*. Azygos nerve. *h*. Ganglion. *i*. Lateral branch of azygos, uniting with postero-lateral nerve *g*. *e*. Antero-lateral nerve. *f*. Medio-lateral nerve. *k*. Hepatic nerve. P. Pyloric. C. Cardiac portion of stomach.

cord immediately behind the œsophagus (Fig. 75, *c*). The size and form of the anterior thoracic ganglion would lead to a suspicion of the complex nature which development shows it to possess. It supplies the somites and their appendages from the fourth to the ninth inclusively, and sends forwards delicate filaments to the œsophagus.

Posteriorly it is connected with the ganglionic mass of the tenth somite by two commissures, and the other thoracic ganglia are similarly brought into communication, the commissures of the ultimate and penultimate only being

remarkable for their brevity. The abdominal, which are much smaller than the thoracic ganglia, are, with the exception of the last two, united by single cords, which represent coalesced double commissures. Each of these ganglia supplies the muscles and the appendages of the somite to which it belongs, and the posterior abdominal ganglion sends branches into the telson.

The Crayfish possesses a remarkably well-developed system of *visceral* or *stomatogastric* nerves, which has been the subject of special study by Brandt, Milne-Edwards, Krohn and Schlemm, each of whom has described a larger or smaller portion of the system with accuracy, but has omitted to mention, or has denied, the existence of some other part. Each of the great commissures (Fig. 75, *b*), as it passes over the sides of the œsophagus, becomes slightly swollen, and from the enlargement four nerves arise; one, external, passes towards the mandibular muscles; a second postero-lateral branch (Fig. 75, *g*) runs upwards and backwards to the infero-lateral regions of the stomach, and eventually enters into the composition of the hepatic nerve (*k*); a third branch (*f*) turns directly inwards and upwards, and unites upon the œsophagus with its fellow and with an azygos nerve (*d*) which passes up in the middle line of the anterior face of the œsophagus and stomach, and enters a ganglion placed between the anterior gastric muscles (*h*), from whence a lateral branch is given off on each side, while a posterior median branch (*d*) continues the direction of the azygos nerve. Having reached the cardiac ossicle, this nerve divides into two branches (*i*), each of which passes downwards and outwards, unites with the postero-lateral nerve of its side, and thus forms the hepatic nerve (*k*). The fourth and last, or antero-lateral branch (*e*) descends at first to near the mouth, and then curving forwards, ascends to unite on the anterior face of the œsophagus with the anterior continuation of the azygos nerve, which passes forwards and upwards and enters the cerebral mass. I am inclined to think that this part of the azygos nerve forms a portion of a

fine plexus of nervous filaments which pass from the cerebral ganglia backwards to the lining membrane of the carapace, but the dissection of these fine filaments and the demonstration of their continuity is a matter of no ordinary difficulty.

The intestine is supplied by two nerves which arise from the last abdominal ganglion, and unite into a single trunk, from which small branches are given off backwards, and two principal ones forwards, which supply the greater part of the intestine. According to Brandt, the genitalia receive branches of the fourth, fifth, and sixth thoracic ganglia.

The only certainly known organs of sense in *Astacus* are the eyes and the auditory organs. The eyes are seated at the extremities of the ophthalmic peduncles, the integument of the outer extremity of which becomes translucent over a reniform space, and constitutes the corneal membrane. This membrane is divided into a great number of minute quadrilateral facets, each of which corresponds with the base of a crystalline cone.*

The upper face of the trihedral, proximal, and largest joint of the antennule presents an oval space, covered by a broad brush of complex hairs having their points all directed inwards. On cutting these hairs away close to their bases, however, it is seen that they cover an aperture, wider above than below, and about one-sixteenth of an inch long. The hairs are attached to the outer lip of this aperture, and some are directed so as to lie within the inner lip, but the majority cover it. A good-sized bristle passes with great ease into this aperture, and if the inner and outer walls of the basal joint of the antennule be now removed, and the soft parts carefully dissected away, the end of the bristle will be seen to have passed into a wide delicate sac about one-twelfth of an inch long, which is attached by a narrower neck round the

* Mr. E. T. Newton's careful description of the eye of the Lobster in 'The Quarterly Journal of Microscopical Science' for 1875, to which I have referred above, may be taken as a guide to the study of the minute structure of the eye in the Crayfish.

aperture, the lips of which are continuous with its walls. The sac is filled with minute sandy particles, suspended in a mucous, dirty-looking fluid, and when emptied of these contents a band, consisting of several lines of very fine hairs, like those which guard the mouth of the sac, but more delicate, is seen to skirt its inner contour. The hairs, projecting inwards, come into close contact with the solid particles suspended in the mucous fluid.

A nerve may be traced accompanying the antennulary nerve to the sac, and appears to be distributed principally along the setigerous band, so that the extremities of the nerve fibrils come into close relation with the bases of the hairs. Some, if not all, of the sandy particles are insoluble in strong acetic acid, and would appear to be silicious.*

Two glandular sacs commonly known as the *green glands*, which were formerly regarded as the auditory organs, lie in the cavity of the head. An aperture is visible on the inner or oral side of a conical prominence, upon the inferior portion of the coxal joint of the antenna. A bristle passed into this aperture enters a large but very delicate and transparent sac, filled with a clear fluid, which is usually conspicuous on each side of the anterior end of the stomach, when the carapace is carefully removed. A nerve which comes off from the cerebral mass close to the antennary nerve, passes to the neck of this vesicle, and is distributed over its surface between the outer and inner membranes, of which it is composed. Inferiorly the vesicle rests upon a large greenish apparently glandular mass, but is directly connected with the latter only at two points, firstly by a vascular cord, which passes to the central, and usually more yellow portion of the gland, and secondly by a short neck-like continuation of the sac itself, which is attached over a small circular space, midway between the centre and the periphery of the gland, and opens into the circular

* See for a full account of the minute structure of the auditory organs in the higher Crustacea, Hensen's 'Studien über das Gehörorgan der Decapoden,' 1863.

principal duct of the gland. There is, therefore, a free communication between the cavity of the gland and the exterior by means of the sac, which is, in this respect, simply a dilated duct. A section of the gland shows it to be composed of two substances, a central and a cortical. The latter is composed of minute cæca, filled with a homogeneous gelatinous matter, containing many large nuclei; the former is traversed in all directions by large canals, so as to have a spongy appearance. The cæca open into the ultimate ramifications of the canals, and the spongy, lung-like texture of the central mass seems to arise merely from the very free anastomosis of their larger branches, which eventually enter the circular canal which communicates with the vesicle.

There is little in these structural features to suggest an organ of special sensation, but much to show that the green mass is a secreting organ, and that the vesicle acts (whatever other purposes it may subserve) as its duct. In all probability the green gland is an organ of the same nature as the shell gland of the *Entomostraca*.

Leydig has attributed an olfactory function to certain groups of delicate setæ which occur on the joints of the outer division of the antennule of the Crayfish.

The most remarkable part of the muscular system of the Crayfish is the great extensor muscle of the abdomen, a complex mass of fibres which is attached in part to the endophragms of the thorax in front, and, behind, to the sterna of the abdominal somites, a large part of the cavity of which it occupies.*

The essential parts of the reproductive organs in the male and female *Astacus* are very similar to one another in form, both ovarium and testis having the figure of a trilobed gland, situated immediately behind the stomach, and below the heart. Two of the lobes are applied together, and pass

* For details, see Suckow, 'Anatomisch-Physiologische Untersuchungen.' Milne-Edwards has described the muscles of the Lobster at length in the 'Histoire naturelle des Crustacés,' tom. i.

forwards; the other lobe is directed in the middle line backwards. The ducts take their origin, one on each side, at the junction of each antero-lateral with the posterior lobe.

In minute structure, however, the two organs differ widely. Each lobe of the testis is composed of a number of small cæca, in which the spermatozoa are developed, and which open into a central duct. The ovarium, on the other hand, is essentially a wide sac, produced into three large cæca, each of which corresponds with a lobe; and the ova are developed in the epithelial lining of the sac. The efferent ducts, again, have little resemblance, the oviducts being short, wide tubes which open on the coxopodites of the antepenultimate thoracic appendages, while the vasa deferentia are canals as long as the body, at first very narrow, but afterwards widening, which lie coiled up on either side of the posterior part of the thoracic cavity, where their white contents make them very conspicuous (Fig. 74, *gn'*). Eventually, they open on the coxopodites of the posterior thoracic appendages.

The spermatozoa, like those of many other *Crustacea*, are motionless, and have the form of cells, provided with a nucleus and produced into several delicate radiating processes. They are united in their course down the vas deferens into cylindrical masses, which becoming invested by a fine membranous coat, probably secreted by the walls of that duct, constitute the spermatophores, which may not unfrequently be found adhering to different parts of the body, not only of female but of male Crayfish.

The ova are fecundated while still within the parent; they become surrounded in their passage down the oviduct, by a coat, corresponding with that of the spermatophore, which is produced into a pedicle, the extremity of which becomes attached to one or other of the abdominal appendages. Great numbers of ova, attached in this way, may be observed during the breeding-season, within the incubatory chamber formed by the flexure of the abdomen upon itself; and it is in this cavity that the embryos pass through the whole of their fœtal existence.

The development of the Crayfish has been the subject of one of the most beautiful of the many admirable memoirs on development, for which we are indebted to the genius and patience of Rathke.* After fecundation a blastoderm arises upon the surface of the yelk, and gradually extending over the whole yelk, becomes thickened at one part, so as to form an oval germinal disk, with a central depression.

This disk next becomes widened and bilobed at its anterior extremity, the lobes being identical with the procephalic lobes, to be hereafter described in the embryo of *Mysis*. The edges of the disk are raised into a fold, and within the fold a papilla, the rudiment of the abdomen, and of the greater part, if not of the whole of the thorax, makes its appearance, while, anteriorly, three pairs of transverse elevations constitute the rudiments of the antennules, the antennæ, and the mandibles. The labrum arises as a median papilla, situated at first between the antennules. The ocular peduncles are next developed in front of the antennules as ridges, which only subsequently become free processes.

The thoracico-abdominal process lengthens, and the anal aperture makes its appearance. It is to be remarked, that the anus is at first situated on the dorsal side of the extremity of the abdomen, and that there is no telson. This is developed only at a much later period from the dorsum of the end of the abdomen; and, by its outgrowth, forces the anus to the ventral side of the body.

In the meanwhile, the oral aperture is developed behind the labrum, which moves backwards; while the maxillæ, maxillipedes and ambulatory feet appear in succession as elevations or ridges of the substance of the embryo, which are, at first, all alike, and gradually become specialised into their ultimate forms.

* 'Ueber die Bildung und Entwickelung des Flusskrebses,' Bd. 29. See also Lereboullet, 'Recherches d'embryologie comparée sur le développement du Brochet de la Perche et de l'Ecrevisse,' 1862; and the account of Bobretsky's researches in Hofmann and Schwalbe, 'Jahresbericht' for 1873 (1875).

When these appendages first appear, the maxillæ and first pair of maxillipedes are attached to the embryo in front of the thoracico-abdominal process, the second maxillipedes lie in the angle between them, and the third maxillipedes and following appendages are attached to the sternal surface of the thoracico-abdominal process itself; and, as this process is at first bent forwards upon the rest of the germ, it follows that the appendages attached to it look upwards, while those attached to the anterior part of the embryo look downwards. As development proceeds, however, the embryo gradually straightens itself; more and more of the anterior part of the thoracico-abdominal process becoming continuous in direction with the anterior part of the embryo; until, at length, the whole of the cephalo-thoracic portion forms a convex surface, parallel with the vitellary membrane, only the abdomen remaining bent upon the cephalo-thorax. The middle portion of the carapace is formed by the continuous calcification of the dorsal walls of the cephalo-thorax of the embryo. Its pleura are developed as two distinct folds, one of which, the rudiment of the branchiostegite, encircles the embryo posteriorly, and extends forwards on each side as far as the mandibles; while the other, the rudiment of the rostrum, and anterior cephalic pleura, is developed in front of the eyes, and extends on each side to meet the former. Rathke's clear account of this matter is in perfect accordance with what I have observed in *Mysis*, and shows conclusively that the carapace is not developed from any one or two somites in particular, but that its tergal portion corresponds with, and is formed by, the terga of all the cephalo-thoracic somites, while the branchiostegites and rostrum are developments of the lateral portions of all these somites; in fact, represent their pleura, which, like the terga, are connate and continuously calcified.

The appendages are thus, at first, similar to one another, and each consists of a ridge which eventually takes the form of a plate, free at the outer end. This plate, in all the

members, except the ophthalmic peduncles and the mandibles, then becomes bilobed externally, the inner lobe representing the endopodite, while the outer is the representative of the exopodite and epipodite. The two latter, when they are independently developed, become separated by the division of the outer lobe. The gills arise partly as outgrowths from the epipodites, partly as distinct processes from the parts to which they are eventually attached. The division of the limbs into articulations takes place from their distal towards their proximal ends. The heart appears late, at the posterior extremity of the cephalo-thorax, and therefore behind the yelk sac.

The nervous system of the post-oral portion of the cephalo-thorax consists at first of eleven pairs of ganglia, corresponding with the mandibles, maxillæ, maxillipedes, and ambulatory legs. The six anterior post-oral ganglia of each side soon coalesce in pairs, so as to form as many single ganglia; and of these the four anterior, namely, the mandibular, the two maxillary, and the first maxillipedary ganglia, unite into a single mass; the two hinder ganglia, that is to say, those of the second maxillipedary somite, next coalesce in the same way, and it is only subsequently that the two masses thus formed become fused into the single anterior post-oral ganglion of the adult. The other ganglia not only remain separate, but become wider apart with advancing age. A ridge on each side of the œsophagus at first represents the cerebral ganglion and the commissural cords, the latter being developed out of the posterior part of the ridge, and the former from its anterior portion. The cerebral ganglia are at first two on each side, but the posterior, whence the nerves to the antennary organs proceed, is much larger than the other, and would appear to represent two ganglia. The endosternites arise as processes from each of the eight posterior cephalothoracic sterna, which eventually arch over the ganglionic cord, and unite with one another.

The alimentary canal is produced by the gradual differentiation and demarcation of the sternal part of the

hypoblast, which invests the whole yelk, from the tergal part, which becomes the yelk sac.*

After the liver, genitalia, and antennary glands are developed, the yelk sac eventually becomes reduced to a small cæcal diverticulum, situated at the pyloric end of the stomach. The genital ducts in both males and females are originally diverticula from the corresponding regions of the genital glands; their external apertures and the copulatory appendages of the first abdominal somites in the male are not developed until some time after birth.

The modifications of structure observable within the limits of the *Podophthalmia* are exceedingly interesting.

Excluding, for the present, the *Squillidæ*, the group is divisible on clear morphological grounds into the following subdivisions:—1. The *Brachyura*; 2. The *Anomura*; 3. The *Macrura*; 4. The *Schizopoda*.

The morphological relations of the *Macrura* are nearly such as are indicated by their position in this series; and *Astacus*, as a central genus of the central group, thus becomes a sort of natural centre for the whole of the *Podophthalmia*, whence we may trace a gradual series of modifications, leading on the one hand to the *Schizopoda*, with their large abdomen and small cephalo-thorax; and on the other to the *Brachyura*, with their rudimentary abdomen and comparatively enormous cephalo-thorax.

In all the *Macrura*, the branchiæ are numerous, and are covered by the branchiostegites. The abdomen is large, and is used as a locomotive organ, the appendages of its sixth somite being well developed. The thoracic ganglia usually form an elongated chain, and the external maxillipedes never form broad opercular plates over the other jaws.

* According to Bobretsky (*l.c.*) there is no proper yelk-sac, the structure so termed by Rathke being the saccular hypoblast, which is formed by invagination of the primitive blastoderm and encroaches upon the vitellus, until the latter is all absorbed. The hypoblastic sac is converted into the liver and the intestine. The stomach arises independently by invagination of the epiblast.

In some of the lower *Macrura* (*Peneus*, *Pasiphæa*), the exopodite persists as an appendage at the base of the thoracic limbs; and in two genera, *Sergestes* and *Acetes*, the posterior thoracic members become rudimentary or even entirely abortive, though the abdominal appendages remain.

In the higher *Macrura*, such as *Palinurus*, the nervous system exhibits a greater degree of concentration, the thoracic ganglia constituting an elongated oval mass; and it is in this genus and its allies that the head and its appendages exhibit modifications, which prepare us for those which are presented by the *Brachyura*. In this respect the *Palinurus vulgaris* (Rock Lobster, Sea Crayfish, or Spiny Lobster) is particularly worthy of attention. The rostrum is rudimentary and represented by a mere spine, leaving the anterior cephalic somites uncovered. The cephalic flexure is so strong as to throw the ophthalmic sternum, which is very wide, completely to the top of the head. The basal joints of the antennæ, or coxocerites, are enormous, fixed to the surrounding parts, and united by their anterior extremities in the middle line below. Superiorly, they seemed to have coalesced with the antennulary sternum, so as to form a projecting wedge-shaped mass, which separates the antennules from the ophthalmic sternum, and causes them to appear, at first, as if they were inferior to the antennæ. In this genus, the basicerite, ischiocerite, and merocerite are much thicker and stronger than the corresponding joints of any of the other appendages; and in the closely allied *Scyllarus*, the facial region of which is, on the whole, similarly constructed, these joints become extremely expanded and flattened, and are succeeded by no procerite. In these genera the scaphocerite, or squame, usually attached to the base of the antenna, is absent; and, in *Scyllarus*, there is another approximation to Brachyuran structure in the existence of distinct orbits, formed by a lobe of the carapace, which descends on the inner side of the ocular peduncle, to meet the base of the antenna. No median septum is formed by the rostrum, however, nor are the antennules capable of being folded

back into distinct chambers in any Macruran at present known.

The *Anomura* are so completely intermediate in structure between the *Macrura* and the *Brachyura*, that they need not be specially noticed, except to draw attention to the singular deviation from the ordinary habits and form of the higher Crustaceans, presented by the *Paguridæ*, or Hermit Crabs, so common on all coasts. Essentially Macruran in their organisation, these *Crustacea* are distinguished from all true *Macrura* by the uncalcified and soft condition of the integument of their unsymmetrical abdomen, the appendages of which are for the most part abortive, those of the sixth somite being modified so as to serve as claspers. It is by means of these that the Hermit Crab retains firm hold of the columella of the empty gasteropod shell into which it is his habit to thrust his unprotected abdomen, and covering over his retracted body with the enlarged chela, which takes the place of an operculum, resists all attempts at forcible extraction.

The internal structure of the *Brachyura* is, on the whole, similar to that of the *Macrura*; but the thoracic ganglia have coalesced to a much greater extent than in *Astacus*, forming a single rounded mass. The branchiæ are few, never exceeding nine on each side, and sometimes not more than seven. The branchiostegite fits closely down upon the bases of the four posterior pairs of thoracic limbs, and sometimes encloses a space which is very large in proportion to the branchiæ. This is particularly the case in the Land Crabs (*Gecarcinus*), where the spacious branchial chamber is lined by a thick and vascular membrane, which, in these almost wholly terrestrial *Crustacea*, either takes on to some extent the respiratory function, or serves to keep the air within the branchial chamber saturated with moisture.

The abdomen in the *Brachyura* is comparatively small; its sixth somite possesses no appendages; and the others, if they exist at all, subserve only a sexual purpose, the two anterior pairs commonly forming accessory copulatory

organs in the male; while, in the female, so many of these appendages as remain give attachment to the ova, which are carried about until hatched, between the thorax and the abdomen, which is bent up against it. The female *Brachyura* also possess a spermatheca attached to each oviduct, which is absent in the *Macrura;* and, in this sex, the abdomen is larger and broader than in the males. In accordance with the rudimentary condition of this part of the body, the abdominal ganglia are represented only by a cord, which proceeds from the posterior part of the great thoracic mass. It is in the construction of their skeleton, however, that the *Brachyura* present the most interesting deviations from the *Macrura*. Thus, if we select the common Shore-crab, *Carcinus mœnas* (Fig. 76), as a typical example of a Brachyuran, we find that the carapace is a wide shield, broader than long, having a somewhat pentagonal shape, and bent sharply inwards at the sides, instead of taking an even sweep down to the base of the legs. It is in such close contact with the four posterior pairs of thoracic limbs, as to leave no passage or aperture such as exists in *Astacus,* the only inlet for the water required for respiration being placed above the basal joints of the chelate anterior ambulatory limbs. The edges of the carapace pass completely in front of the bases of the limbs, and then turn suddenly forwards, parallel with one another and with the axis of the body, as the *pterygostomial plates* of Milne-Edwards, to join the antennary sternum, which is very wide, but short from before backwards. The space included between the edges of the pterygostomial plates and the antennary sternum is the "cadre buccal," or *peristome;* the antennary sternum itself receives, as in the *Astacus,* the specific appellation of *epistoma;* and the plate which stretches backwards and supports the labrum, within its posterior forked boundary, is the *endostoma.*

The middle of the dorsal surface of the carapace is marked somewhat nearer its posterior than its anterior boundary by a short transverse depression, which is continued on each side forwards and outwards, and then curves directly out-

wards to the edge of the carapace (Fig. 76, *c s*). Further than this I cannot trace this homologue of the cervical

Fig. 76.

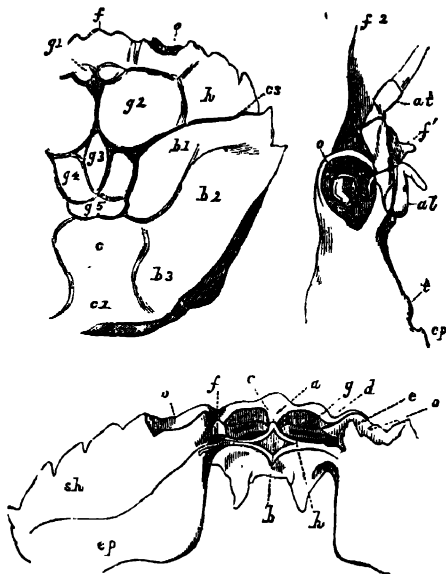


Fig. 76.—Of the two upper figures the left represents the dorsal surface of the carapace of *Carcinus mænas*. *f*. Rostrum. *o*. Orbit. *c. s*. Cervical groove. g^1. Epigastric lobe. g^2, Protogastric. g^3. Mesogastric. g^4. Hypogastric. g^5. Urogastric. *c* c^1. Anterior and posterior cardiac. *h*. hepatic. b^1, b^2, b^3. Epibranchial, mesobranchial, and metabranchial lobes. The lower figure represents a ventral view of the anterior half of the same carapace. *a*. Rostral septum. *b*. Antennary sternum. *c*. Suture between these. *d*. Supraciliary lobe. *e*. Internal suborbitar lobe. *f*. Antenna. *g*. Articular cavity for the ophthalmic peduncle. *h*. The same for the antennule. *o*. Orbit. *sh*. Subhepatic region. *ep*. Anterior pleural region. The right-hand upper figure gives a side view of the carapace of *Stenorhynchus phalangium*, the common "spider-crab." *o*. Orbit. f^1, f^2 Rostrum. *al*. Antennule. *at*. Antenna. *ep*. Epistoma.

groove of *Astacus*. Elevations and depressions upon the surface of the carapace in front of the cervical groove,

which, as in *Astacus*, is composed of the connate terga of the six cephalic somites, mark it out into certain definite regions of considerable systematic importance. An irregular transverse depression, crossing the carapace near the anterior margin, bounds an anterior or facial region, divided into a middle *frontal* lobe (*f*), and lateral *orbital* lobes (*o*), from a posterior, much larger, gastro-hepatic area, divided into small lateral *hepatic* lobes (*h*), and a large complex *gastric* lobe (g^1, g^2, etc.). The latter is again subdivided into two *epigastric* lobes (g^1), two *protogastric* lobes (g^2), a median *mesogastric* lobe (g^3), two *metagastric* lobes (g^4), and two *urogastric* lobes (g^5), making altogether nine subordinate divisions. The gastric lobes correspond in a general way to the stomach; the hepatic lobes, to a portion of the liver. The region behind the cervical suture consists of the connate terga of the eight thoracic somites; it is divided by two strong longitudinal grooves, the *branchio-cardiac* grooves, into a middle region, corresponding with the heart, and two lateral regions, forming the roof of the branchial chamber. A transverse depression divides the middle region into an anterior and a posterior cardiac lobe, while the *branchial* region is subdivided into *epibranchial* (b^1), *mesobranchial* (b^2), and *metabranchial* (b^3) lobes.

On turning to the inflected inferior portion of the carapace, a sutural line or groove is seen running from the epistoma, outwards and backwards, very nearly reaching the outer edge of the carapace, opposite its external angle, and then sweeping backwards parallel with, and but little distant from, its postero-lateral boundary, until it cuts its posterior edge. The portion of the carapace internal to this sutural line, is called by Milne-Edwards the *inferior branchiostegite*, and is considered by him to be composed of an anterior (*e p*) and posterior *epimeral* piece, corresponding with the *sub-hepatic* (*s h*) and *sub-branchial* regions of the surface of the carapace between the suture and the line of inflection. I cannot regard these parts, however, as having any relation with the true epimera. The suture, or rather

groove, seems rather to correspond with that which marks off the pleuron from the rest of the somite in *Astacus*.

The anterior cephalic somites in *Carcinus* have undergone some singular modifications, whereby their true relations are greatly obscured. The broad trilobed plate (Fig. 76, *f*) corresponds with the elongated rostrum of *Astacus*; inferiorly it is produced in the median line into a strong ridge or septum, the lower and posterior edge of which is convex, and fits closely into the concavity formed by the antennulary and ophthalmic sterna, as they bend back from the sternal flexure. This rostral septum, therefore, abuts below and behind on the epistoma, and constitutes a sort of partition (Fig. 76, *a*), by which the cavities in which the antennules and eyes of the two sides are lodged, are completely separated from one another. The lateral portions of the rostrum form a flattened roof over the inner portions of these cavities, which contain the bases of the ophthalmic peduncles and the antennules; but the outer angles of the rostrum are produced downwards (*d*), to form the *supraciliary lobe*. The outer half of the lateral cavities or chambers is more excavated, and is bounded by a strong pointed process, the *external orbitar* lobe, which is divisible into a *supra-orbital* and *sub-orbital* portion. The latter passes gradually into a strong process of the sub-hepatic region, called the *internal sub-orbitar* lobe (Fig. 76, *e*); this turns forwards and upwards towards the supraciliary lobe, which it approaches, but does not meet, the base of the antenna being, as it were, wedged between the two.

The supraciliary, external orbitar, and internal sub-orbitar lobes, and the antennæ, thus together circumscribe a cavity widely open in front, which is called the orbit, inasmuch as it lodges the terminal portion of the ophthalmic peduncles, with the eyes which they support. The proximal portions of the peduncles pass through the comparatively narrow opening by which the inner and outer chambers communicate, between the antenna and the supraciliary process, and are inserted as usual into the

articular cavities on each side of the ophthalmic sternum, which is narrow, and hardly wider than the septum. It thus comes to pass that the eyes, lodged in their orbits, appear to be altogether external to the antennules, the enlarged bases of which hide the ophthalmic peduncles, and appear to be the sole contents of the inner division of the sub-frontal chamber; but the true position of the eyes is precisely the same as in *Astacus*, that is to say, anterior and superior to the antennules. Another interesting peculiarity about the facial region of the carapace is that the basal joints of the antennæ have coalesced with the sternum of the antennary somite, and, consequently, that the bases of the antennæ are immoveable. There is no vestige of a scaphocerite, and the aperture of the organ which answers to the green gland of *Astacus*, is provided with a peculiar moveable plate, provided with a projecting internal stem, to which delicate muscles are attached in *Carcinus*. It is this structure which has been compared to an auditory ossicle; but, as in *Astacus*, the auditory sacs are, in fact, lodged in the dilated basal joint of the antennule.

A cervical fold, lodging the scaphognathite, occupies the same relative position as in *Astacus*, and marks off the cephalic from the thoracic region, on the sides of the body. The thoracic sterna gradually increase in breadth, and the posterior ones are marked externally by a strong median, longitudinal depression, answering to a corresponding fold on the inner surface. The apodemal cells are well formed, but the sternal canal, so largely developed in the *Macrura*, is absent in this, as in all other *Brachyura*.

The structure of the appendages is essentially the same as in *Astacus*, but the third thoracic appendage, or external maxillipede, has its ischiopodite and meropodite greatly enlarged, so as to form a broad plate, which, with its fellow, covers over the other organs, and hence receives the name of the *gnathostegite*. The three terminal joints of the limb remain small, and constitute a palpiform appendage—the *endognathal palp*.

In some of the lower *Macrura*, the thoracic limbs are provided with a short exopodite, and the posterior maxillipedes become indistinguishable from the ordinary thoracic limbs. Such forms lead us naturally to the *Schizopoda*, a group the name of which is derived from the apparent splitting of the limbs produced by the great development of the exopodite, which, in these *Crustacea*, is as large as the endopodite. In this group, again, a line can hardly be drawn, in many cases, between any of the maxillipedes and the thoracic limbs, the anterior pair only being somewhat smaller than the rest. Hence *Thysanopoda* is admitted, by Milne-Edwards, to have eight pairs of thoracic limbs ('Crustacés,' ii. 464). The branchiæ in the *Schizopoda* are frequently absent; when well developed, as in *Thysanopoda*, they are not included under the branchiostegite, but hang down freely from the bases of the thoracic limbs. In *Mysis*, the only representative of a branchia (if it be one in reality) is a process attached to the first thoracic appendage. *Cynthia* has its branchial appendages attached to the abdominal members.

In *Thysanopoda*, *Mysis*, and *Cynthia*, the general structure of the body is similar to that of the *Macrura*, except that, in *Mysis*, the greater number of the abdominal appendages are rudimentary.

In *Leucifer*, the antennary somite is produced into a very long and narrow peduncle, which supports the eyes, on their great stalks, the antennules, and the antennæ, at its extremity, separating them from the rest of the cephalothorax, which is covered by a delicate carapace, bent down at the sides. The anterior thoracic members are rudimentary, and the posterior pair is absent. The heart is short and rounded, and situated, as usual, in the thorax.

It has been seen that in *Astacus fluviatilis*, as in *Limulus* and *Daphnia*, the embryo slowly and gradually passes into the form of the adult; to which it is so similar when it leaves the egg, that the changes of the young present nothing comparable to the well-known metamorphoses of Butterflies and Beetles.

But most *Podophthalmia* rather resemble the *Copepoda* and the majority of the *Entomostraca*, in the fact that the young, when they leave the egg, have a totally dissimilar form to that of the parent, and only acquire the adult condition after a series of ecdyses.

The observations of Fritz Müller * have shown that the young of a species of Prawn (*Peneus*) undergo a metamorphosis which runs parallel with that of the *Copepoda*.

Fig. 77.

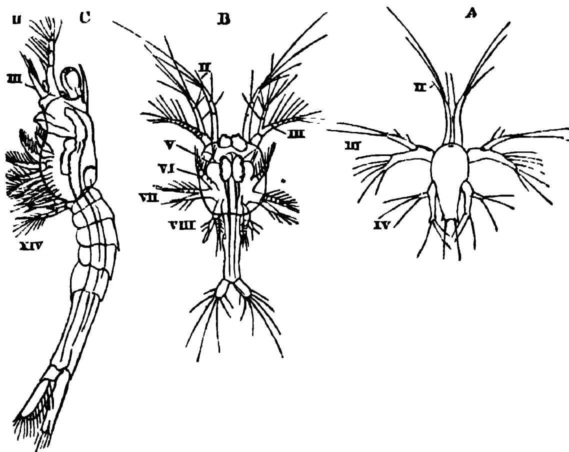


Fig. 77.—*Peneus.*—A, *Nauplius*-stage. B, *Zoœa* or Copepod stage. C, *Schizopod*-stage. (After Müller.)

When it leaves the egg (Fig. 77, A), the young *Peneus* has an oval, unsegmented body with a single frontal eye, a large labrum and three pairs of natatorial appendages—it is in fact, to all intents and purposes, a *Nauplius*. The *Nauplius*-form next developes a rounded tergal shield, or carapace; the first and second pairs of appendages remaining long, become the antennules and the antennæ; while those of the third pair, their bases enlarging at the expense

* 'Für Darwin,' 1864.

of the rest of the appendage, become the mandibles. Four pairs of appendages subsequently appear behind the mandibles. The hinder three pairs are bifurcated and become the two pairs of maxillæ and the first and second maxillipedes. Behind these again are five pairs of short lamellar processes, which eventually are converted into the rest of the thoracic appendages. The six somites of the abdomen are long and distinct, and the last ends in two setose processes. They are at first without appendages. In this stage (Fig. 77, B), which answers to the so-called *Zoœa*-form of other *Podophthalmia*, the principal locomotive organs are the antennæ and antennules, and the resemblance to an adult Copepod is so striking that it may be termed the *Copepod* stage. Next, the antennæ, diminishing in relation to the rest of the body, cease to be the principal organs of locomotion, and the rapidly elongating abdomen assumes that function. The stalked double eyes which made their appearance in the Copepod stage, become more fully developed. The jointed exopodite of the antenna is replaced by a single plate. The greatly enlarged thoracic limbs are provided with an endopodite and an exopodite, as in the *Schizopoda*, the branchiæ are developed from them, and the abdominal appendages make their appearance. This may be termed the *Schizopod* stage (Fig. 77, C). Lastly, the median eye vanishes, the exopodite of the locomotive thoracic limbs disappears, and the larva assumes all the characters of the adult *Peneus*.

In the great majority of the *Podophthalmia* the embryo undergoes as remarkable a metamorphosis after it leaves the egg. This fact was first indicated by Siebold, afterwards demonstrated by Vaughan Thompson, whose observations have been confirmed and extended by many more recent observers, notably by Spence Bate * and Claus. † But the stages of this metamorphosis differ from those

* "On the Development of Decapod Crustacea." (Philosophical Transactions, 1857.)

† "Zur Kenntniss der Malakostracenlarven." (Würzburg 'Naturwissenschaftliche Zeitschrift,' 1861.)

observed in *Peneus* in the apparent absence of the first or *Nauplius* condition. Possibly, however, this is represented by a delicate cuticular investment which the larva throws off soon after leaving the egg. It then corresponds with the later form of the Copepod stage of *Peneus*, and is termed a *Zoœa*. The *Zoœa* has a short carapace, often provided in the median frontal and dorsal regions with long spine-like prolongations. There is a median simple eye between the lateral sessile faceted eyes, a pair of antennules, a pair

Fig. 78.

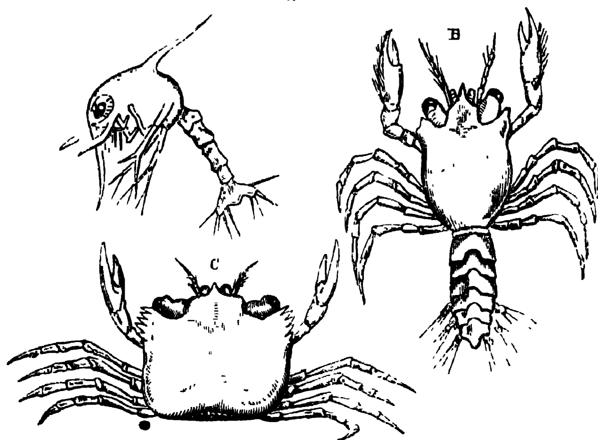


Fig. 78.—Development of *Carcinus mœnas*. A. *Zoœa*-stage. B. *Megalopa*-stage. C. Final state. (After Couch.)

of antennæ, a pair of mandibles, and two pairs of maxillæ; in short, all the appendages of the head. Of the appendages of the thorax, the first two pairs are well developed, and terminate in an exopodite and an endopodite. But behind these, which become the first and the second pair of maxillipedes, only short rudiments of the six remaining pairs of thoracic appendages are to be found, and the somites of the long abdomen have no appendages at all. Subsequently these make their appearance, the posterior thoracic

members increase in size, the eyes become raised upon short peduncles, and the larva resembles one of the lower *Macrura*. The carapace next becomes broader, and its spines shorter, while the ambulatory thoracic limbs take on the characters of those of the adult, the bifurcated first and second pairs becoming metamorphosed into the first and second maxillipedes. The abdomen becomes relatively short and slender, and the larva takes on the characters of one of the *Anomura*. In this stage it has been named *Megalopa*. By further changes in the same direction, the Anomuran condition passes into that of the young Brachyuran. All these modifications of form are accompanied by exuviations of the chitinous cuticula.

The successive stages are well exemplified by the young of the Shore-crab, *Carcinus mœnas* (Fig. 78, A, B, C). The larva, on leaving the egg, has sessile eyes, a long pointed rostrum, and a spine projecting from the middle of the carapace; rudimentary antennæ, and two pairs of locomotive appendages — the rudiments of the anterior maxillipedes. The abdominal somites are without appendages, and the telson is broad and bilobed (Fig. 78, A).

This, the *Zoœa* stage, after repeated ecdyses, assumes the *Megalopa* form represented in Fig. 78, B. Finally, the carapace becomes broader, the abdomen loses its appendages, and is bent up under the thorax; the peculiarities of the facial region, characteristic of the *Brachyura*, are developed; the antennules and ambulatory members acquire their characteristic proportions; and the little Brachyuran by degrees assumes the special peculiarities of *Carcinus* (Fig. 78, C).

The development of the Opossum Shrimp (*Mysis*)* is particularly interesting, as it appears to indicate the relations between the two modes of development, that with and that without metamorphosis, which obtain in the *Crustacea* (Fig. 79).

The ova consist of a vitelline mass, enclosed within a delicate chorion. The blastoderm appears as an oval patch

* Conf. E. van Beneden, "Développement des Mysis." ('Bulletin de l'Académie de Bruxelles,' 1869.)

upon the surface of the yelk (Fig. 79, A, *c*), thickest in the middle, and here presenting a more or less marked depression (Fig. 79, A, B, *c*). It is sharply defined from the subjacent yelk (*b*), and consists of a finely granular mass, in which multitudes of nuclei, about $\frac{1}{1800}$ to $\frac{1}{2000}$ of an inch in diameter, are imbedded.

The blastoderm next becomes larger at one end than at the other, and a median sinuation gradually divides this extremity into two lobes, which will eventually form the anterior parietes of the head, and may be called the *procephalic lobes.**

The median depression becomes more decided, and, at the end opposite the procephalic lobes, the blastoderm is produced into a sort of papilla, directed forwards. This is the rudiment of the caudal extremity. From the anterior part of the blastoderm there arise, on each side, two papillæ, the points of which are directed backwards, and which will become the antennules and antennæ. The whole of these parts are invested by a delicate cuticular membrane, which gradually extends over and invests the whole yelk beneath the vitellary membrane. At the end of the caudal papilla it forms a broad process, produced into setæ, which sometimes appear fan-like, sometimes so deeply bifid as to resemble two styles.

The embryo has now reached what we may term its larval stage, and, in this condition, it leaves the vitellary membrane within which it was enclosed, and lies free in the ovigerous pouch of the parent. At the same time, the caudal extremity enlarges, and straightens itself out, so that no indication of its previous inflexion against the thoracic portion of the blastoderm remains. The larva thus much resembles a pear

* It is exceedingly interesting to remark the correspondence between the embryonic structure of the head of *Mysis* (and I may add that of other *Arthropoda*), and that of the head of a vertebrate embryo. The procephalic processes resemble in a remarkable manner the *trabeculæ cranii* of the vertebrate embryo; and the cephalic flexure of the Crustacean or Insect has its analogue, if not its homologue, in the angle which the trabecular region of the base of the skull at first makes with the parachordal region in almost all *Vertebrata*.

(Fig. 79, D, E), with four processes (2, 3), the antennules and antennæ, which have now become much elongated, on one surface.

The young *Mysis* next grows rapidly and undergoes great changes in form: but it is a very remarkable fact, that the primitive integument remains unaltered; gradually enlarging, to accommodate itself to the increased size of the fœtus, indeed, but otherwise taking no share whatever in its changes. The young *Mysis* might, therefore, in this condition be justly termed a pupa, for the relation of the primitive integument to the animal which it encloses is precisely that of the pupa skin to the imago of an insect.

Fig. 79.

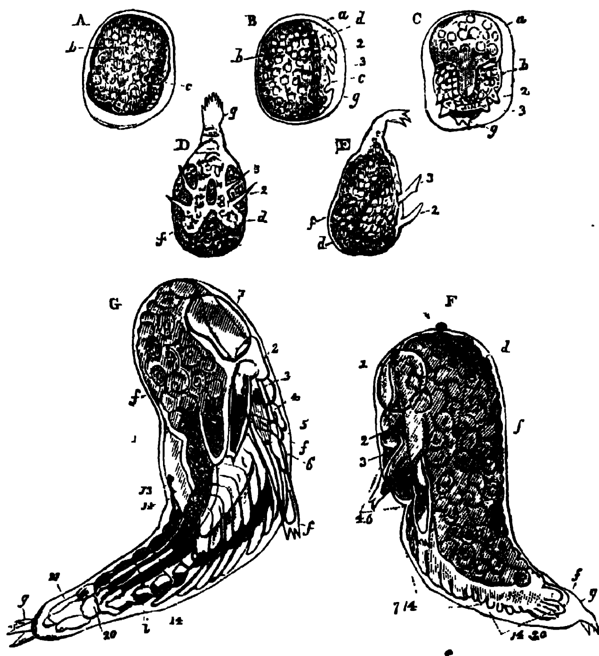


Fig. 79—*continued.*

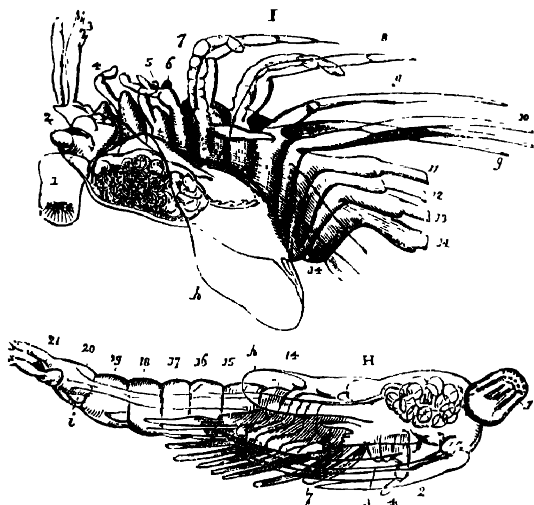


Fig. 79.—The development of *Mysis.*—A. Side view of an egg, in which the blastoderm has just appeared. B. Side view further advanced. C. Front view of embryo at the same age, showing the procephalic lobes, here marked *b.* D. Larva, ventral view. E. Side view. (These two figures have been inverted by the engraver.) F. Young pupa. G. Further advanced. H. Young *Mysis*, which has left its pupa skin. I. Anterior portion of the same, enlarged, and with the carapace thrown back. *a.* Vitelline membrane. *b.* Yelk. *c.* Central depression of the blastoderm. *d.* Procephalic lobes. *f.* Larval integument. *g.* Its caudal enlargement. *h.* Carapace. 1, 2, 3, 4, etc. the somites and their appendages, numbered from before backwards.

The antennules and antennæ remain intact within the sheaths afforded by the primitive integument, but, becoming immensely elongated and divided at their extremities, assume more and more their proper adult conformation.

In front of the antennules, a large rounded protuberance makes its appearance upon each procephalic lobe, and eventually becomes the ophthalmic peduncle. At first, the sternal portions of the somites, corresponding with these three pairs of appendages, occupy the same plane with one

another and the posterior sterna (Fig. 79, F, G); but, by degrees, they become bent up (Fig. 79, H), and at length the ophthalmic sternum occupies the upper and front part of the head (Fig. 79, I). In this way the "cephalic flexure" is produced. The mouth is indicated[1] behind the antennary sternum, which projects backwards in the middle line to form the labrum. On each side of it the rudiments of the mandibles appear, and behind these are the papillary commencements of the two pairs of maxillæ. Behind the second pair of maxillæ, a distinct constriction indicates the commencement of the thorax, the appendages of which appear, at first, as tubercular elevations, all of precisely the same character, and all directed backwards parallel with one another. The abdomen is at first very small, and the appendages of its sixth somite early acquire a far larger size than the others. The telson is developed from the middle line above the anus. While all these changes are going on, the blastoderm gradually extends over the tergal surface of the embryo and closes it in. When the carapace is first distinguishable it appears as a ridge arising from the sides of the posterior thoracic somites, beginning at the last but one, and gradually extending forwards as far as the antennary somites. The ridge increases and becomes a fold, which overhangs the bases of the thoracic appendages (Fig. 79, G); and if this fold be turned back (Fig. 79, I), its actual attachments may be readily demonstrated.

Having advanced thus far in its development, the fœtal *Mysis*, with all its organs fully formed, though somewhat different in appearance from those of the adult, casts its pupa-skin and straightens its body, which from having its posterior portion bent on the anterior, as in the embryo (Fig. 79, B) had gradually in the pupa (Fig. 79, F, G) assumed the opposite curvature. Its dimensions are threefold those of the embryo, and it exhibits vivacious movements when extracted from the pouch of the parent. It is not improbable it may yet undergo another change of integument before acquiring the full form of the adult.

Thus it appears that in *Mysis*, the *Nauplius*-stage (Fig. 79, D, E) is passed over so rapidly that the embryo has gone through it at a very early period, and nothing but the cuticular sheath of the body appertaining to this stage remains to prove its existence. A step further, in the abbreviation of the *Nauplius*-stage, and there would be nothing

Fig. 80.

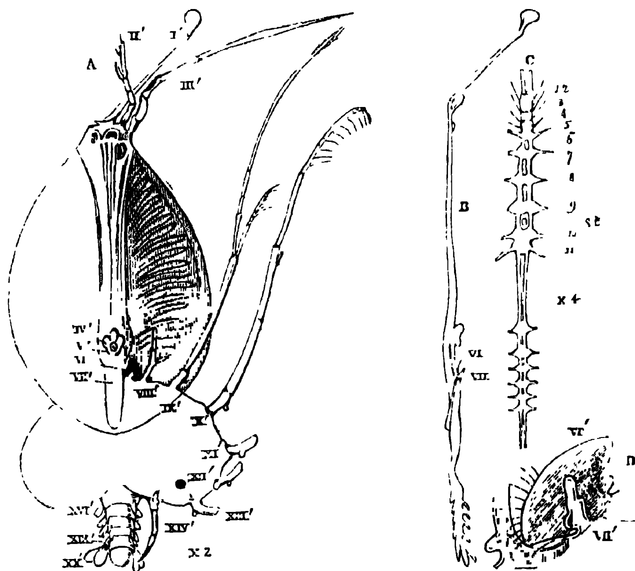


Fig. 80.—*Phyllosoma*.—A, ventral view of the body with the limbs I'—XX' of the left side and the bases only of XI' to XIII' represented; B, side view of the body; C, the nervous system; D, the last cephalic, and first and second thoracic limbs.

to distinguish the general course of the development of *Mysis* from that of *Astacus*. On the other hand, another Schizopod, *Euphausia*, has been shown by Metschnikoff * to leave the egg as a true *Nauplius*.

* 'Zeitschrift für Wiss. Zool.,' 1871.

The Glass-crabs, or *Phyllosomata* (Fig. 80), are singular marine pelagic crustacea, in which the body consists almost wholly of two large, extremely flat and transparent disks, devoid of any segmentation. The anterior of these bears the pedunculated eyes, the antennules and the antennæ on its anterior margin; while the labrum, with the mandibles and anterior pair of maxillæ, form a small projection posteriorly on its ventral surface. The second pair of maxillæ is situated a little more backwards and outwards, and bears a scaphognathite; and just behind these appendages is the fold of a cervical groove which separates the anterior disk from the posterior. The anterior disk contains the stomach and the liver, and in this respect, as in its appendages, corresponds exactly with the cephalostegite of the carapace of an ordinary Crustacean, and its six cephalic sterna. The posterior disk, on the other hand, contains the short and almost round heart, with the intestine, and bears the eight pairs of thoracic appendages, the anterior and posterior of which are not uncommonly rudimentary. The abdomen is usually very small, and situated in a notch at the posterior edge of the thoracic disk. It is provided with six pairs of appendages. No generative organs have been found in the *Phyllosomata*, and there is reason to believe that they are merely larvæ of the Macruran genera *Palinurus*, *Scyllarus*, *Thenus*, and their allies.

The CUMACEA.—These are very remarkable forms, allied to the *Schizopoda* and *Nebalia*, on the one hand, and on the other to the *Edriophthalmia* and *Copepoda*; while they appear, in many respects, to represent persistent larvæ of the higher *Crustacea*.

Cuma Rathkii might, at first, be readily mistaken for a Copepod. It possesses a comparatively small thick carapace, apparently produced into a rostrum anteriorly, and succeeded by a series of twelve gradually narrowing free segments, the appendages of which are in great part obsolete. The last of these segments is a pointed telson; the

anterior five, belonging to the thorax, bear thoracic limbs, while the eleventh, the last true somite of the body, carries its characteristic styliform appendages. The appendages of the preceding abdominal somites may be either absent or very small and rudimentary. Dohrn has proved that this is true only of the females among the *Cumacea*. The males, which were formerly referred to the genera *Bodotria* and *Alauna*, often have well-developed abdominal limbs, though they appear late. It is interesting to find that the females, in this respect, retain more of the larval character than the males.

On examining the apparent rostrum with care, it is found to be divided along the middle line by a fissure which runs in front of the eye (which is here single and sessile) divides into two branches, which run backwards and outwards, and terminate, before traversing half the length of the carapace; they thus cut off a median lobe, bearing the eye at its apex, from two lateral processes. The lateral processes are simply prolongations of the antero-lateral regions of the posterior division of the carapace (as it were the antero-lateral angles of the carapace of *Mysis*, excessively produced and meeting in the middle line); while the middle lobe corresponds, I believe, with the cephalostegite of the carapace in ordinary *Podophthalmia*, the insertions of the mandibular muscles occupying their normal position, towards its posterior boundary. The hinder part of the carapace will therefore correspond with the terga of the three anterior thoracic somites, the five posterior ones being, as has been seen, free and moveable.

The five anterior pairs of thoracic appendages are constructed much on the same plan as those of the *Schizopoda*; the three posterior have no exopodite. In the female, the sixth abdominal somite alone has appendages, but in the male the two anterior abdominal somites are provided with styles. Ovigerous plates are attached to the fourth, fifth, and sixth thoracic appendages in the female. The structure of the head is peculiar. No ophthalmic sternum nor ophthalmic peduncles are discernible, the single, or closely

approximated two, eyes being sessile on the median line on the superior surface of the head. The coxopodites and basipodites of the antennules and antennæ are bent down almost at right angles with the axis of the body, and appear to be connate, or confluent, with their sterna. The succeeding joints are free and pass forwards, the antennules being much longer and stronger than the antennæ in the females, while, in the males, the antennæ are very long; the labrum is large; the mandibles strong and unprovided with a palp. There is a distinct metastoma, and the maxillæ are delicate and foliaceous. A papillose branchial plate is attached to the base of the first thoracic appendage. The surface of many parts of the body in some species exhibits a very peculiar sculpturing, singularly like that exhibited by the *Eurypterida*.

As in the *Podophthalmia*, the heart is short or moderately elongated, and situated in the posterior part of the thorax.

Dohrn* has shown that the development of the *Cumacea* takes place without metamorphosis. In most respects the embryo resembles that of *Mysis*; but, instead of the cuticular investment of the transitory *Nauplius*-stage with its two pairs of appendages, there is only a sort of cuticular sac with a thickening in the middle line of the tergal aspect, which the embryo bursts as it acquires a larger size. In this respect, the resemblance of the embryonic development of the *Cumacea* to that of the *Edriophthalmia* is, as Dohrn points out, very striking, and no doubt they form a connecting link between the *Podophthalmia* and the *Edriophthalmia*. Having regard to their whole organisation, on the other hand, they stand at the bottom of the Malacostracan group, and are comparable to a *Peneus*-larva in the Copepod stage, the limbs and body of which are modified in the direction of the *Schizopoda*, while the fore part of the head has remained Copepodous.

Fossil *Brachyura* are abundant in tertiary deposits, but are rare in formations of earlier date. *Macrura* of a pecu-

* "Ueber den Bau und die Entwickelung der Cumaceen." ('Untersuchungen über Bau und Entwickelung der Arthropoden,' 1870.)

liar type (*Eryon*) occur in the mesozoic rocks, and perhaps the carboniferous *Gampsonyx* should be referred to the *Podophthalmia.*

The EDRIOPHTHALMIA.—These resemble the *Podophthalmia* in never possessing a greater than the typical number (20) of somites, though, in some members of the group, the body is composed of fewer somites, in consequence of the abortive or rudimentary condition of the abdomen. Eyes may be absent; when present, they are usually simple, and are either sessile or seated upon immoveable peduncles (*Munna*). The antennules almost disappear in the terrestrial *Isopoda*, while the antennæ become rudimentary or vanish in some *Amphipoda.* The mandibles lose their palps in the Woodlice; which thus, as in the presence of only one pair of well-developed antennary organs, approach Insects. Ordinarily, the posterior seven, and, at fewest, the posterior four, thoracic somites are perfectly distinct from, and freely moveable upon, one another. The ophthalmic and antennary somites have coalesced with the rest of the head; the branchiæ depend from the thoracic limbs, or are modifications of the abdominal appendages; and the heart is elongated and many-chambered. But the salient characters of the group will be best understood by the study of such a genus as *Amphithoe*, the principal details of the organisation of which are represented in Fig. 81.

The body of this animal is compressed, bent upon itself, and divided into fifteen very distinct segments, reckoning the head as the first and the telson as the last.

The head presents a rounded tergal surface; the anterior face is disposed perpendicularly to the axis of the body, and is produced anteriorly into a strong, curved, and pointed rostrum; on each side, it bears an aggregation of simple eyes, and, in front, immediately beneath the rostrum, this face gives attachment to two long, many-jointed antennules. Below these, two antennæ, shorter, and fewer-jointed than the antennules, are inserted, and the inferior part of the face is completed by a large moveable labrum. Behind

this come the strong, toothed palpigerous mandibles (IV′),

Fig 81.

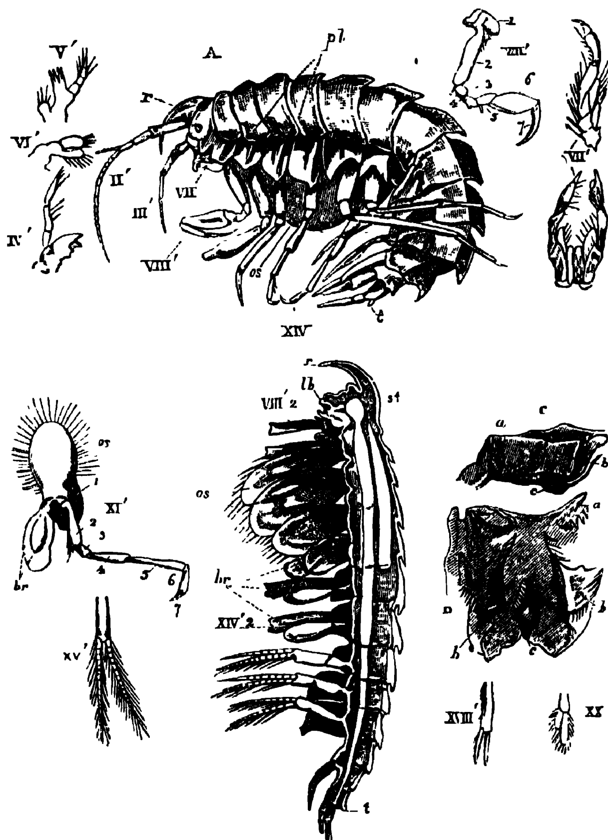


Fig. 81 —*Amphithoë*.—The letters and figures have the same signification as in other figures of Crustacea except *os*, oostegite. *Br*. branchiæ. C. Lateral view of stomach (D) opened from above. *a*, *b*, *c*. Different parts of the armature.

and two pairs of more or less foliaceous maxillæ. Inas-

much as the eyes are sessile, these five pairs of appendages are all that belong to the head proper; but, just as in the *Podophthalmia*, certain of the anterior thoracic appendages are converted into accessory gnathites, so, in *Amphithoe*, the first pair of these members are applied against the mouth, and form a large lower lip (VII').

The "head" of *Amphithoë*, therefore, is formed by the coalescence of the seven anterior somites of the body; but I believe that the tergum of the seventh (or first thoracic) somite is obsolete, as in a Stomatopod, and hence that the tergal surface of the head of the *Edriophthalmia* corresponds exactly with the cephalostegite (or that part of the carapace which lies in front of the cervical groove) in *Podophthalmia*. Mr. Spence Bate has shown, in his valuable 'Report on the *Edriophthalmia*,' that, in the *Crustacea* at present under discussion, a strong apodeme arises on each side from the posterior part of the sternal region of the head, and passing inwards and forwards meets with its fellow, to form an endophragmal arch, which supports the œsophagus and stomach, and protects the nervous commissure between the first and second sub-œsophageal ganglia, which runs under it.

The discoverer of this structure conceives that it represents the terga of the three somites immediately succeeding the mouth; but I cannot see that it is other than the representative of the precisely similar mesophragm formed by the anterior apodemes in *Astacus*. In fact, the correspondence in structure between the head of an *Amphithoe* and the cephalic portion of the cephalo-thorax of *Astacus* is not a little striking. There is the same sternal flexure, the same relative position of the stomach, and of the insertions of the mandibular muscles. The great difference lies in the abortive condition of the ophthalmic appendages.*

* A strong endophragmal arch separates the sub-œsophageal ganglia and commissures from the gullet in *Squilla*, but has different connexions (Fig. 83). A very similar endophragmal arch is found in the Insect head. See the description of the head of *Blatta* (*infrà*).

The seven free somites of the thorax each give attachment to a pair of limbs. It is characteristic of *Amphithoe*, as of the *Amphipoda* in general, to have the five anterior pairs of thoracic members directed forwards. Each limb consists of an expanded coxopodite, succeeded by the other six joints of the typical crustacean limb.

In the male, a single vesicular lamella, the branchia, is attached to the inner side of the coxopodite of the appendages of the ninth to the fourteenth somites inclusively; but, in the female, an additional plate, convex externally and concave internally, is attached above and internal to, the branchia of the 9th to the 12th somite. These *oostegites*, as they may be called, enclose a cavity in which the incubation of the eggs takes place.

The abdomen consists of six somites and a very small terminal telson. The appendages of the three anterior somites are terminated by two multiarticulate setose filaments (Fig. 81, XV′) while in the three posterior, the corresponding parts are styliform, and serve as a fulcrum for the abdomen when the animal leaps, by the sudden extension of that region of the body.

The *Edriophthalmia* are ordinarily divided into three groups. The *Amphipoda*, which resemble *Amphithoë*, are characterised by their compressed form and their ordinarily saltatory habits; by having thoracic branchiæ; by the forward direction of their four anterior locomotive limbs (2nd to 5th pairs of thoracic appendages), and by the contrast between the three anterior and the three posterior pairs of abdominal appendages. The common Sand-hopper is the most familiar example of this division. The second group is that of the *Læmodipoda*, distinguished by the rudimentary state of the abdomen, which is reduced to a mere papilla, and by the coalescence of the second, as well as the first, thoracic somite with the head, so that the anterior limbs appear to be as it were suspended under the neck. The strangely formed genera *Cyamus*, the parasite of whales, and *Caprella*, which is very common upon our own

coast, adhering to corallines, sea-weeds and starfish, belong to this group.

The *Isopoda*, which constitute the third group of the *Edriophthalmia*, are usually depressed instead of compressed, and run or crawl instead of leaping. Many, like

Fig. 82.

Fig. 82.—*Cymothoa*.—The letters and figures have the same signification as in Fig. 81, except *Ab*, Abdominal appendages in Fig. A.

the common Woodlouse (*Oniscus*), possess the power of rolling themselves into a ball when alarmed; some, like the last-named genus, are terrestrial; others, like the *Asellus*, inhabit fresh waters, but the great majority are marine; and among them are many peculiarly modified

parasitic forms (Fig. 82, *Cymothoa; Bopyrus*). The composition of the head and mouth in the *Isopoda* is essentially the same as in the *Amphipoda*, though differing considerably in details. The branchiæ of the thoracic members are absent, their functions being performed by the endopodites of some of the abdominal members, which are soft and vascular. The three anterior pairs of thoracic members are usually directed forwards—the four posterior pairs backwards. In some *Isopoda* the abdominal somites, partly or wholly, coalesce with one another.

In all the *Edriophthalmia* the alimentary canal is straight and simple, and its anterior gastric dilatation, frequently strongly armed, is situated in the head. The liver is represented by a variable number of straight cæca.

Occasionally there are one or two cæca which open into the posterior part of the intestine, and appear to be urinary organs analogous to the Malpighian cæca of insects.

The respiratory organs vary greatly in structure. In most *Edriophthalmia*, they are simple plates or sacs, the delicacy of the integument of which permits of the free exposure of the blood circulating in them to the air. In the amphipod genus *Phrosina*, however, the branchiæ are composed of rudimentary lamellæ, attached to an expanded stem, and resemble not a little the epipoditic branchiæ of *Astacus*. In some *Sphæromidæ*, Duvernoy and Lereboullet found the branchial endopodites transversely folded, so as to approach those of the *Xiphosura*.

The exopodites of the abdominal members of the *Isopoda* frequently cover the modified endopodites, forming opercula, and the first pair of abdominal limbs is, in many genera, altered in such a manner as to form one such large operculum for the four pairs which succeed it. In the *Idoteidæ* it is, on the other hand, the sixth pair of abdominal limbs which are so modified as to form the curious door-like opercula which cover the gills.

In certain of the terrestrial *Isopoda*, (*Porcellio*, *Armadillidium*,) some of the opercular plates of the branchiæ, usually the two anterior pairs, contain curiously ramified

cavities, which open externally, and contain air. The genus *Tylos* possesses respiratory organs, which present a still more interesting approximation to those of the purely air-breathing *Articulata*. They are thus described by Milne-Edwards :—

"The abdomen presents inferiorly a deep cavity, very similar to that of the *Sphæromæ*, in which the five anterior pairs of appendages are lodged; but this cavity, instead of being completely open below, is imperfectly closed, in its posterior half, by two series of lamellar prolongations, which arise from the sides of the inferior faces of the third, fourth, and fifth abdominal segments, and pass horizontally inwards; the first pair of these plates is small, those of the third pair are, on the other hand, very wide, and almost meet in the median line. The four anterior pairs of abdominal appendages, lodged in this cavity, each carry a wide and short quadrilateral appendage, the surface of which is raised into a transverse series of large longitudinal elevations, and each of these elevations presents inferiorly a linear aperture leading to a respiratory vesicle, the parietes of which are covered with a multitude of little arborescent cæca. These vesicles when extracted from the interior of the limb closely resemble a brush-like branchia, having its longitudinal canal in communication with the atmosphere by a longitudinal stigma. The fifth pair of abdominal members are rudimentary, while the sixth constitute the door-like triangular valves covering the anus, and all the inferior face of the last abdominal segment." *

The nervous system in the *Amphipoda* consists of supra-œsophageal or cerebral ganglia, united by commissures with an infra-œsophageal mass, whence commissural cords pass under the endophragm to the anterior of the thoracic ganglia, of which there are commonly seven pairs, succeeded by five or six pairs of abdominal ganglia. In some *Isopoda* (*Cymothoa*, *Idotea*) the abdominal ganglia are also distinct; but in others, such as *Æga bicarinata* (according to Rathke), they are fused into a single mass placed in the anterior

* 'Histoire Naturelle des Crustacés,' vol. iii. p. 187.

part of the abdomen, presenting only traces of a division into five portions. In the *Cymothoadæ* and terrestrial *Isopoda*, again, the abdominal ganglia appear to have completely coalesced with the last thoracic ganglia and form a mass, whence the abdominal nerves radiate. Finally, in the short-bodied *Lœmodipoda*, such as *Cyamus*, there are not more than eight pairs of post-œsophageal ganglia, the posterior commissures of which are so shortened that the nervous system ends in the antepenultimate somite.

Brandt describes splanchnic ganglia like the lateral pair of Insects in the *Oniscidæ*. It is one of the many respects in which the *Isopoda* simulate *Insecta*.

No other organs of sense than eyes have, as yet, been certainly demonstrated to exist in the *Edriophthalmia*, though the fine setæ which beset the antennary appendages, have been supposed to be organs of the olfactory sense. The eyes vary in their structure, from the simple, more or less closely aggregated ocelli of *Lœmodipoda*, and of many *Isopoda* and *Amphipoda*, to the strictly compound eyes, as complex as those of the highest *Articulata*, which exist in *Æga* and in *Phrosina*.

The female genitalia of the *Edriophthalmia* consist of two simple sacs, the ducts of which usually open on the ventral surface of the antepenultimate thoracic somite, or on the bases of the limbs of this somite. In the male, one or more cæca on each side constitute the testis, which ordinarily opens on the last thoracic or first abdominal somite, in connexion with one or two pairs of copulatory organs developed from the anterior abdominal somites.

The eggs of the ordinary *Edriophthalmia* usually undergo their development in the chamber beneath the thorax enclosed by the oostegites of the thoracic appendages. In most cases, the young differ so little from the adults that no metamorphosis can be said to take place. They frequently, however, want the last thoracic somite. The young of the parasitic *Edriophthalmia*, such as *Bopyrus*, *Phryxus*, *Cymothoa*, *Cyamus* and the *Hyperinæ*, on the other hand, are

widely different from the adults; and not only in their metamorphosis, but in the small proportional size and less aberrant form of the male, *Bopyrus* and *Phryxus* recall the parasitic *Copepoda*.

In certain Amphipods (*Gammarus locusta* and *Desmophilus*) the vitellus undergoes complete division; while, in closely allied forms (*Gammarus fluviatilis* and *pulex*), and still more completely in those *Isopoda* which have been studied, the part of the vitellus which divides into blastomeres, becomes more or less completely separated from the rest immediately after fecundation, and the so-called partial yelk division, take place.*

In all *Edriophthalmia*, the development of which has been examined, before any other organs appear, a cuticular investment or sac is formed, which is eventually burst and thrown off. This appears to represent the *Nauplius* cuticle of *Mysis*, and, in close relation with it, are peculiar tergal structures, such as the bifid lamellæ of *Asellus* and the unfortunately named "micropyle apparatus" of other *Edriophthalmia*.

The *Edriophthalmia* are not abundant in the fossil state; but they may be traced back as far as the later Palæozoic strata (*Prosoponiscus*, *Amphipeltis*).

The STOMATOPODA.—Of the *Stomatopoda* of Milne-Edwards, two of the three divisions, the *Caridoides* and the *Bicuirassés* have since found a place among the Schizopodous *Podophthalmia*, or among the larvæ of certain *Macrura*; but the third, the *Stomatopodes unicuirassés*, comprising *Squilla*, *Gonodactylus*, and *Coronis*, appear to me to differ so widely and in such important structural peculiarities, not only from the *Podophthalmia* proper, but from all other *Crustacea*, as to require arrangement in a separate group, for which the title of *Stomatopoda* may well be retained.

* E. van Beneden, 'Recherches sur la Composition et la Signification de l'Œuf,' 1870.

The genera named, in fact, stand alone among the *Crustacea*,* in that the ophthalmic and antennulary somites are complete rings, moveable upon one another and the

Fig. 83.

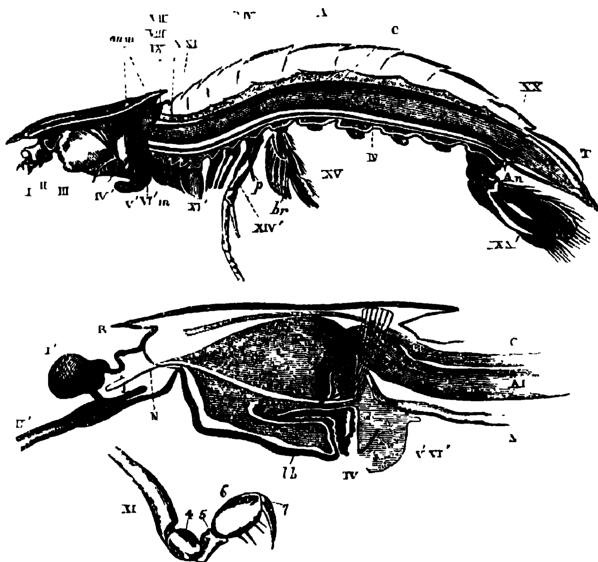


Fig. 83. — *Squilla scabrıcauda.*—A, the entire body, with the thorax and abdomen in longitudinal and vertical section; B, the head in vertical section. I-XX, somites of which the body is composed. I'-XX', their appendages, the bases of most of which are alone represented. AL, alimentary canal; G, stomach; *An*, anus; C, heart; *br*, branchia. N, ganglia and their commissures. R, rostrum of the carapace; *p*, the penis. *Pn*, endophragmal arch. The fifth thoracic appendage XI' is figured separately.

antennary somite, and that their long axis is parallel with

* Unless the freedom of the anterior segment of the head in the *Pontellidæ* referred to above, when the *Copepoda* were under consideration, is a parallel case.

that of the body, so that there is no sternal flexure. Numerous pairs of hepatic cæca open into the elongated alimentary canal. The heart again is not short and broad, with at most three pairs of apertures and confined to the thoracic region, as in the proper *Podophthalmia*; but it is greatly elongated, multilocular, and extends into the abdomen. The branchiæ are plumes attached to the abdominal members (Fig. 83, A, *br*), and, so far as I have been able to ascertain, the carapace is, in all, connected exclusively with the cephalic somites. This is particularly well seen to be the case in *Squilla scabricauda* (Fig. 83), where five completely developed posterior thoracic terga can be counted, uncovered by the short carapace, beneath which the terga of the three anterior thoracic somites are represented by a membrane which passes forwards to be reflected into the carapace.

The free somites of the thorax, and those of the abdomen, in this species and in the *Stomatopoda* generally, are so large relatively to the carapace, that the latter is not larger in proportion to the body than the tergal covering of the head in many *Edriophthalmia*, with which order the *Stomatopoda* present many marked affinities. Indeed, if we leave the eyes out of consideration, the organisation of the *Stomatopoda* is more Edriophthalmian (and especially Amphipodan) than Podophthalmian. The five anterior pairs of thoracic members are turned forwards, and are subchelate. The first pair are small and slender. The second pair are the largest of all, and have the characters of powerful prehensile limbs, the terminal curved and spinose joint of which shuts down into a groove in the penultimate joint, as the blade of a pocket knife does into its handle. The three posterior thoracic limbs, on the other hand, are turned outwards, and terminated by an endopodite and an exopodite.

Squilla lays its eggs in burrows in the bottom of the sea, which the animals inhabit. The earliest condition of the free larva is not fully known, but the young larvæ have a single eye, and the hinder thoracic and the abdominal

appendages are not developed.* The larvæ pass into forms which under the names of *Alima*, *Erichthys*, and *Squillerichthys*, were formerly considered to be independent genera. Claus's investigations, however, have rendered it probable that the two latter genera are simply larval stages of *Gonodactylus*, and that *Alima* is a larval stage of *Squilla*.

* Fritz Müller, 'Fur Darwin.' See also Claus, 'Die Metamorphose der Squilliden,' 1872.

CHAPTER VII.

THE AIR-BREATHING ARTHROPODA.

AMONG these *Arthropoda*, no forms absolutely devoid of limbs are at present known, though the appendages are reduced to two pairs of minute hooks in the vermiform parasite *Linguatula*.

The ARACHNIDA have pediform gnathites, and the least modified forms of this group (the *Arthrogastra* or Scorpions and Pseudo-scorpions) exhibit, in many respects, extraordinarily close resemblances to the *Merostomata* among the *Crustacea*.

The ARTHROGASTRA.—The anterior part of the body of a Scorpion (Fig. 84) presents a broad shield-like tergal plate, resembling that of *Eurypterus* in form. Two large eyes are situated one on each side of the middle line of the shield, while smaller eyes, which vary in number according to the species, are ranged along its antero-lateral margins.

Six wide plates, representing the terga of as many somites, follow the anterior shield, and are connected only by the soft integument of the sides of the body with their sterna. The seventh is united with its sternum (XV) posteriorly, while the five following terga and sterna form continuous rings, which constitute the joints of the so-called "tail." The anus is situated behind the last sternum. A moveable terminal piece, answering to the telson of a Crustacean, which is swollen at its base, and then rapidly narrows to a curved and pointed free end, overhangs the anus, and constitutes the characteristic weapon of offence

of the Scorpion. This sting, in fact, contains two glands which secrete a poisonous fluid, and their ducts convey it to the minute aperture situated at the sharp point of the organ. On the sternal surface of the body, there are four

Fig. 84.

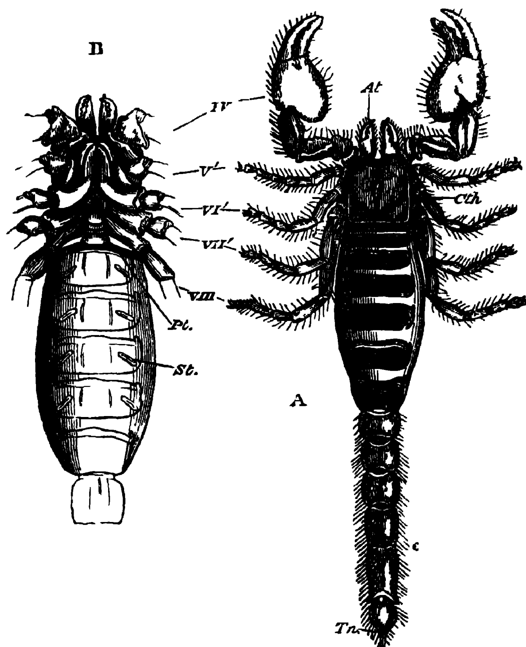


Fig. 84.—*Scorpio afer*.—A, tergal and B, sternal view of the body; *At*, chelicerae, IV', pedipalpi; V', VI', posterior pair of cephalic appendages; VII', VIII', anterior thoracic limbs; *Pt*, pectines; *St*, stigma; *Cth*, cephalo-thorax. (After Milne-Edwards and Dugès.*)

wide and long sternal plates (XI–XIV), which correspond with the third, fourth, fifth and sixth of the free terga. Each of these bears a pair of oblique slits, which are the openings

* 'Règne Animal,' Illustrated Edition.

of the respiratory organs (Fig. 85, *e*). The sterna of the

Fig. 85.

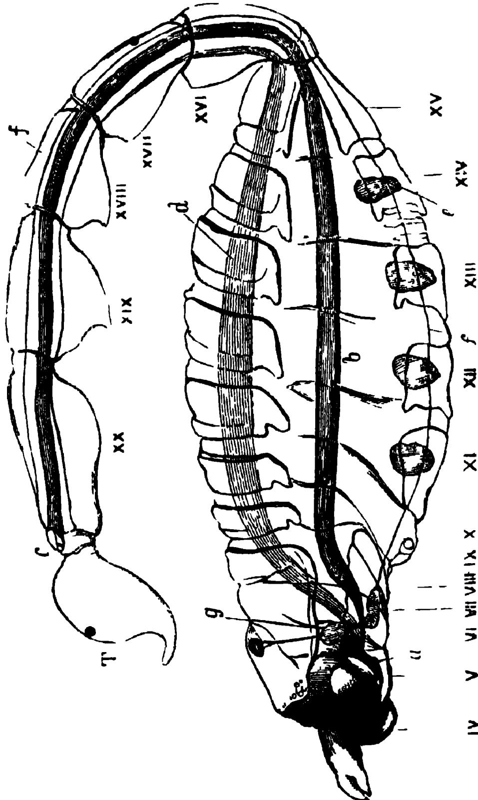


Fig. 85.—A diagram of the body of a Scorpion, the majority of the appendages being removed: *a*, the mouth; *b*, the alimentary canal; *c*, the anus; *d*, the heart; *e*, a pulmonary sac; *f*, the position of the ventral ganglionated cord; *g*, the cerebral ganglia; T, the telson. VII-XX, the seventh to the twentieth somite. IV, V, VI, the basal joints of the pedipalpi, and two following pairs of limbs.

first and second free somites (IX, X) are very small; that of

the first carries the valves which cover the genital aperture; that of the second bears a pair of very curious appendages, somewhat like combs, which are termed the *pectines*. The nervous trunks which enter the pectines are distributed to the numerous papillæ which cover them, and are probably tactile in function. Thus there are twelve somites behind the eye-bearing shield, and none of these are provided with appendages, unless the pectines be such.

The truncated anterior extremity of the body, beneath the shield, is formed by a very large setose labrum, behind and below which, in the middle line, is the extraordinarily minute aperture of the mouth (Fig. 86, M). On each side of it is attached a three-jointed, pincer-ended, appendage, the *chelicera*. Behind these follow the *pedipalpi*, large chelate limbs, the stout basal joints (IV′) of which lie on each side of the mouth.

The following four pairs of appendages are seven-jointed ambulatory limbs, each terminated by three claws. The basal joints of the first two (V′, VI′) lie behind the mouth, the posterior and inferior boundary of which they form, and are directed forwards. The basal joints of the last two (VII′, VIII′), on the other hand, directed inwards, are firmly united together, and are altogether excluded from the mouth.

Thus the mouth is situated between the labrum in front, the bases of the pedipalpi and those of the first two pairs of ambulatory limbs, at the sides and behind; just as in *Limulus*, the mouth lies between the labrum and the basal joints of the third, fourth, and fifth limbs, which answer to the mandibles and first and second maxillæ of the higher *Crustacea*. If this comparison is just, there is one pair of præ-oral appendages, which exist in *Limulus*, wanting in the Scorpion; and the difference between the two may be represented thus:

Limulus.	Antennule.	Antenna.	Mandible.	Maxilla 1.	Maxilla 2.
Scorpio.	Chelicera.		Pedipalpus.	Leg 1.	Leg 2.

Again, if the eye-bearing part of the head may be re-

garded as a somite, then the body of the Scorpion, like that of a malacostracous crustacean, will consist of twenty somites and a telson. We may regard the six posterior somites (XV–XX) as the homologues of those which constitute the abdomen in the crustacean; while the eight middle somites (VII–XIV) will answer to those which enter into the thorax of the latter; and the head will resemble that of an Edriophthalmian with one pair of antennary organs completely suppressed. Upon this view, the eye-bearing shield is a carapace covering a cephalo-thorax, into which the two

Fig. 86.



Fig. 86.—*Scorpio.*—Vertical section of the cephalo-thorax: *At*, chelicera; *lb*, labrum; M, mouth; *a*, pharyngeal sac; N, N', supra- and infra-œsophageal ganglia; *b*, œsophagus; *d*, opening of the salivary ducts; *e*, intestine; H, heart.

anterior thoracic somites only enter. These are followed by six free thoracic somites, the four posterior of which are pulmoniferous. But no trace of the supposed missing antennary appendage has been met with in the embryonic condition, so that the alternative possibility that the mouth is situated one somite further forward in the Scorpion than in the Crustacean must be borne in mind. It is a very interesting fact that Metschnikoff * has found rudiments of

* "Embryologie des Scorpions." ('Zeitschrift für Wiss. Zoologie,' 1871.)

limbs on those somites of the embryo Scorpion on which the stigmata are situated, a circumstance which suggests the suspicion that the Scorpion is derived from some form possessing more numerous limbs.

The minute oral aperture leads into a small pyriform laterally-compressed sac (Fig. 86, *a*) with chitinous elastic walls. Muscles pass from these to apodemes of the sternal wall of the head, and doubtless act as divaricators of the wall of the sac. As the Scorpion sucks out the juices of its prey, it is probable that the elastic sac acts as a kind of buccal pump — the nutritious fluid rushing in when the sides of the pump are separated, and being squeezed into the œsophagus when the elasticity of the walls brings them back to their first position.*

The œsophagus (Fig. 86, *b*) is an exceedingly narrow tube, which springs from the tergal and posterior aspect of the sac just mentioned, traverses the nervous ring, and then, passing obliquely upwards and backwards, enlarges into a dilatation which receives the secretion of two large salivary glands, by a wide duct on each side. The alimentary canal narrows again, and becoming a delicate cylindrical tube which widens posteriorly, passes straight through the body to the anus. The numerous ducts of the liver open into the anterior part of this region of the alimentary canal, and it receives two delicate Malpighian tubuli.

The liver is a vast follicular gland, which occupies all the intervals left between the other organs in the enlarged part of the body, and even extends for some distance into the narrow posterior somites.

The eight-chambered heart (Fig. 86, H) is a larger and more conspicuous structure than the alimentary canal, above which it lies, in a pericardial sinus situated in the middle line of the tergal aspect, between the eye-bearing shield and the tail; each chamber is wider behind and narrower in front, and has two valvular apertures, by which blood is admitted from the pericardial sinus at its postero-lateral angles. It

* Huxley, "On the Mouth of the Scorpion." ('Quart. Journ. of Microscopical Science,' 1860.)

gives off small lateral arteries, and ends in front and behind in a wide aortic trunk. Of these the anterior is larger than the œsophagus, and both aortæ give off branches which are distributed widely through the body. A large trunk lies on the tergal aspect of the ganglionic chain, and is united with the anterior dorsal aorta, by a lateral aortic arch, on each side of the body. The veins, on the other hand, are irregular passages, the blood of which is carried to two *afferent pulmonary sinuses*, one for each set of respiratory organs.

These respiratory organs are four pairs of flattened sacs, which open externally by as many stigmata, on the sterna of the four posterior free thoracic somites (Fig. 85, XI–XIV)

Fig. 87.

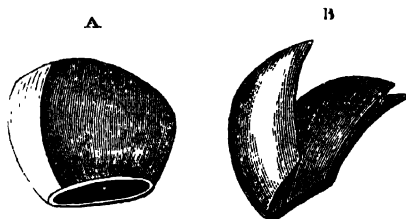


Fig. 87.—A, pulmonary sac; B, respiratory leaflets of *Scorpio occitanus*. (After Blanchard.)

in front of the tail. Each lies with one flat side sternal and the other tergal, in front of its stigma, and its walls are so folded as to divide its cavity into a multitude of subdivisions, each of which opens into the common chamber which communicates with the exterior by the stigma (Fig. 87). The organ, in fact, somewhat resembles a *porte-monnaie* with many pockets. The blood circulates in the folds and, after being thus exposed to the influence of the air, is carried by *efferent pulmonary sinuses* to the pericardial sinus. Expiration is effected by muscles which pass vertically between the sterna and terga of the free somites.

The bilobed cerebral ganglion supplies nerves to the eyes and cheliceræ, and is connected by thick commissures with

the post-œsophageal ganglion, a large oval mass, whence branches are given to the maxillæ and following somites. A long cord formed by two closely-applied commissures passes to the three ganglia placed in the twelfth to the fourteenth somites. There are four ganglia in the abdomen, two distinct cords passing from the last to its extremity. The visceral nervous system is represented by an œsophageal ganglion receiving roots from the cerebral ganglion, and giving branches to the alimentary canal.*

Two lateral ovarian tubes, connected by transverse anastomoses with a median tube, end in two oviducts, which open by a fusiform vagina on the first free sternum (IX). The tubular testes end in a pair of deferent ducts, on which, before their union at the common orifice, two long and two short cæca are found, the former playing the part of vesiculæ seminales. Both male and female organs lie imbedded in the hepatic mass in the posterior thoracic region, their ducts passing forwards. Partial yelk-division takes place, and the ova undergo development within the ovarian canals, in a manner which is very similar to that of *Astacus*. Thus there is no metamorphosis, and the young differ but little from the adult in any respect but size.

The Pseudo-scorpions (*Chelifer*, *Obisium*) resemble the Scorpions in form and in the nature of their appendages, but they have no aculeate telson nor poison gland. They possess silk-glands which open close to the genital aperture, and their two pairs of stigmata are connected, not with pulmonary sacs, but with tracheal tubes. According to Metschnikoff, the eggs undergo complete yelk-division, and the young leave the egg provided only with that pair of appendages which become the pedipalpi.

In the number of the appendages, and in the segmentation of the abdomen, *Galeodes* (or *Solpuga*) agrees with the Scorpions and Pseudo-scorpions. But the three somites which bear the three hinder pairs of ambulatory limbs

* Newport, "On the structure &c., of the nervous and circulatory systems in Myriapoda and Macrurous Arachnida." ('Philosophical Transactions,' 1843.)

(VI, VII, VIII in the Scorpion) retain their distinctness, and there is no cephalo-thorax, in the proper sense of the word. In form and function the pedipalps resemble the first pair of ambulatory limbs, while the cheliceræ are subchelate. The organs of respiration are tracheal.

The *Phalangidæ* (*Phalangium, Gonyleptus*) have chelate cheliceræ, but the pedipalps are filiform or limb-like, and the articulated abdomen is relatively short and broad. They have no silk-glands, and their respiratory organs are tracheal.

Fig. 88.

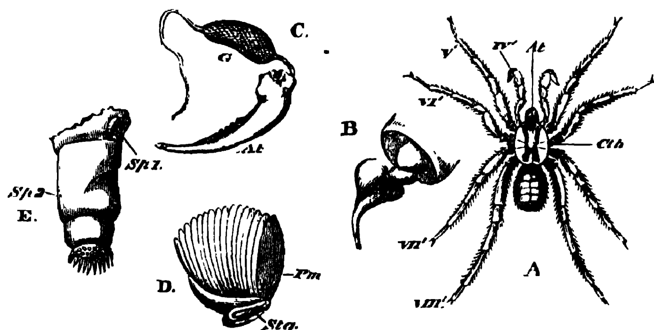


Fig. 88.—*Mygale cæmentaria.*—A female of the natural size: *At.* cheli-

poison gland; D, the left pulmonary sac viewed from its dorsal aspect; *Stg*, stigma; *Pm*, pulmonary lamellæ; E, the two arachnidial mammillæ of the left side, the smaller *Sp*1 is situated on the base of the large one *Sp*2. (After Dugès, 'Règne Animal.')

While the last-mentioned forms lead from the *Arthrogastra* to the *Acarina*, the pulmonate *Phrynidæ*, or Scorpion-spiders (*Thelyphonus, Phrynus*), are in many respects intermediate between the *Arthrogastra* and the *Araneina*.

The ARANEINA.—The Spiders stand in somewhat the same relation to the Scorpions, as the brachyurous to the macrurous *Crustacea*. That part of the body which lies

behind the cephalo-thorax and answers to the free somites of the body of *Scorpio* is swollen, and presents no distinct division into somites.

The cheliceræ are subchelate, that is to say, the distal joint is folded down upon the next, like the blade of a pocket knife upon the handle. The duct of a poison gland, lodged in the cephalo-thorax, opens at the summit of the terminal joint. The pedipalpi are filiform, and, in the males, their extremities are converted into singular spring boxes, in which the spermatophores are received from the genital apertures and conveyed to the female (Fig. 88, B).

The pulmonary sacs, two or four in number, are similar to those organs in *Scorpio*, and are placed in the anterior part of the abdomen; a tracheal system is also present, a pair of sternal stigmata, situated either behind the pulmonary sacs, or at the end of the abdomen, leading into two more or less branched tubes. There is a complex pharyngeal apparatus, probably having the same function as in *Scorpio*.* The stomach gives off cæcal prolongations which may extend far into the limbs. There is usually a dilated short rectum, into which the branched Malpighian ducts open. The nervous system, more concentrated than that of the *Arthrogastra*, is reduced to a supra-œsophageal ganglion and a single post-œsophageal mass, with four indentations on either side. There are six or eight simple eyes in the anterior part of the carapace. Auditory organs have not been discovered in these or any other *Arachnida*.

One of the most characteristic organs of the *Araneina* is the *arachnidium*, or apparatus by which the fine silky threads which constitute the web, are produced. H. Meckel,† who has fully described this apparatus as it occurs in *Epeira diadema*, states that, in the adult, more than a thousand glands, with separate excretory ducts, secrete the viscid material,

* Lyonet's "Anatomie de différentes espèces d'Insectes" ('Mém. du Muséum d'Histoire Naturelle,' 1829) contains an elaborate account of this apparatus, as well as of the structure of the pedipalps of the male spiders.

† "Mikrographie einiger Drüsen-apparate der niederen Thiere." (Müller's Archiv, 1846.) See also Buchholz and Landois. (Ibid., 1868.)

which when exposed to the air, hardens into silk. These glands are divisible into five different kinds (aciniform, ampullate, aggregate, tubuliform, and tuberous), and their ducts ultimately enter the six prominent *arachnidial mammillæ*, which, in this species, project from the hinder end of the abdomen. The superior and inferior mammillæ are three-jointed, the middle one is two-jointed. Their terminal

Fig. 89, A.

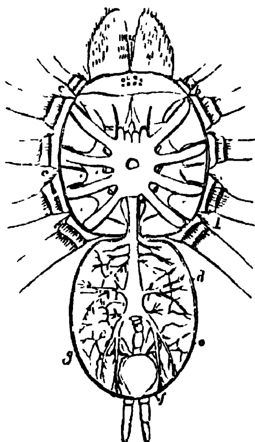


Fig. 89, B.

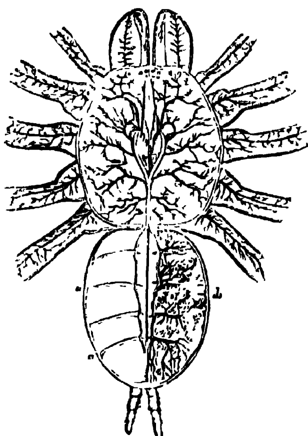


Fig. 89, A.—*Mygale Blondii* (after Blanchard).—The stomach with its cæca, and the remainder of the alimentary canal with the liver and Malpighian tubes.
Fig. 89, B.—The heart and arterial vessels of the same.

faces are truncated, forming an area beset with the minute *arachnidial papillæ* by which the secretion of the glands is poured out.

The males are smaller than the females, and their approaches to the latter are made with extreme caution, as they run the risk of being devoured; extending their pedipalps, they deposit the spermatophores in the female genital aperture, and betake themselves to flight.

The *Araneina* are oviparous, but the development of the embryo takes place as in the *Arthrogastra*, and there is no metamorphosis.*

The ACARINA.—In the Mites and Ticks, the hinder somites are, as in the Spiders, distinctly separated from one

Fig. 90.

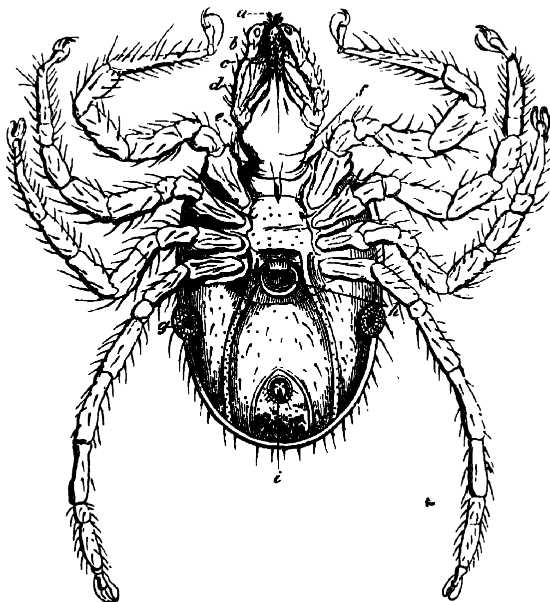


Fig. 90.—*Ixodes vicinus*, female (after Pagenstecher).†—*a*, mandibular hooklets; *b*, *d*, *e*, fourth, third, and second joints of the palp; *c*, hooklets of sternal surface of proboscis; *f*, base of the proboscis; *g*, stigma; *h*, genital aperture; *i*, anal valves.

another, but they are not separated by any constriction from the anterior somites.

* Claparède, "Recherches sur l'Evolution des Araignées," 1862. Also Balbiani, 'Ann. des Sc. Nat.' 1873.

† 'Anatomie der Milben,' 1860.

The bases of the cheliceræ, and of the pedipalpi, coalesce with the labrum, and give rise to a suctorial rostrum (Fig. 90).

There are usually several gastric cæca, but no distinct liver. Salivary glands occur in some, and Malpighian cæca are occasionally found. No heart has yet been discovered. Special respiratory organs are sometimes wanting (*e. g. Sarcoptes*); when present, they are tracheal tubes, springing brush-wise from a common trunk which opens by a stigma. The stigmata are usually two, sometimes anterior and sometimes posterior in position. The ganglia of the nervous system are concentrated round the gullet, as in the Spiders; and the reproductive aperture is situated far forwards, sometimes close to the rostrum.

The greater number of the *Acarina* are parasites upon other animals or upon plants.

Most are oviparous, but the *Oribatidæ* are viviparous. The course of the development of the embryo is the same as in the Spiders. The young, when born, are frequently provided with only three pairs of ambulatory limbs, the fourth pair making its appearance only after ecdysis has occurred.

In some *Acarina*, a singular kind of metamorphosis occurs.

Thus, in *Atax Bonzi*, Claparède * observed that, before the limbs appear on the blastoderm, a chitinous cuticula is separated and forms an envelope, which he terms the "sac of the deutovum." The proper vitelline membrane bursts into two halves, much as in *Limulus*, and the deutovum emerges. In the meanwhile, the anterior end of the blastoderm becomes fashioned into two procephalic lobes; while five pairs of tubercles, answering to the rudiments of the cheliceræ, pedipalpi, the two posterior gnathites, and one pair of thoracic limbs of the Spiders, make their appearance beneath the sac of the deutovum. The rudiments of the chelicerae and pedipalpi apply themselves together, and coalesce into a proboscis. Thus the first larval form is completed. It tears the pseudoval sac, emerges, and buries itself in the

* "Studien an Acariden." ('Zeitschrift für Wiss. Zoologie, 1868.)

branchiæ of the freshwater mussel (*Unio*), upon which it is parasitic. The cuticular investment of the first larva now becomes distended by absorption of water, and forms a globular case, the limbs being drawn out of their sheaths. The second larval stage completes itself within the sac formed by this singular ecdysis. The two palpi are deve-

Fig. 91.

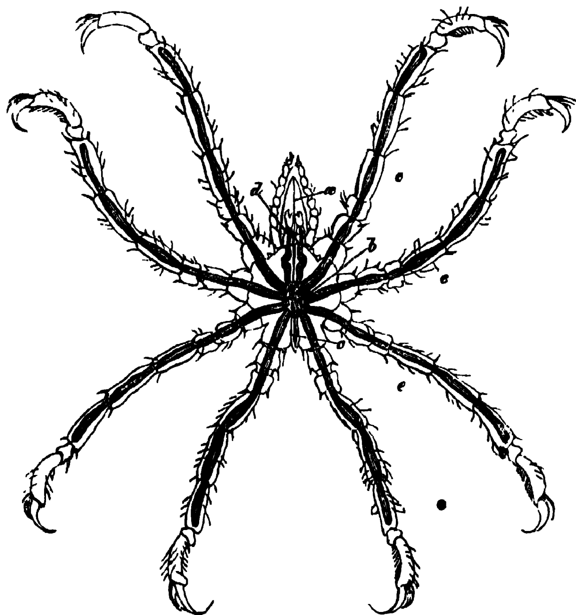


Fig. 91.—*Ammothea pycnognoides*, female (after Quatrefages).—*a*, œsophagus; *d*, antennæ; *b*, stomach with its prolongation into the antennæ and limbs *e*; *c*, rectum.

loped from the pedipalpal portion of the proboscis; two horny hooks from the cheliceral portion; and, finally, the hinder pair of thoracic limbs is added. This second larva gradually passes into the adult *Atax*.

In the Acarus (*Myobia coarctata*) of the Mouse, Claparède

observed that the deutovum stage is followed by a tritovum; the chitinous sac, which invests the embryo within the deutovum, apparently representing the cuticle of the first larva of *Atax*. In this case, it presents a parallel to the *Nauplius* cuticle of *Mysis*.

The *Arthrogastra*, the *Araneina* and the *Acarina* (with some doubtful exceptions among the latter) possess the same number of appendages, and do not differ from one another so much as do the different forms of the *Copepoda*, among the *Crustacea*. But the remaining groups which are usually included among the *Arachnida*; namely, the *Pycnogonida*, the *Arctisca*, and the *Pentastomida*, diverge widely from the *Arthrogastra* and the *Araneina*, though each exhibits certain approximations to the *Acarina*.

The PYCNOGONIDA.—These are marine animals with short bodies terminated in front by a rostrum like that of the Mites, but with a mere tubercle in place of the posterior thoracic and abdominal somites. The adult has four pairs of enormously elongated, many-jointed ambulatory limbs, in front of which are three pairs of short appendages, the anterior of which may be chelate, while the posterior are more or less rudimentary (Fig. 91).

The alimentary canal sends off very long cæca into the legs. There is a short heart, but no distinct respiratory organs exist. A cerebral nervous mass is connected with a ventral chain of four or five pairs of ganglia. Four eyes are seated upon a dorsal tubercle above the brain. The sexes are distinct, and the testes and ovaria are lodged in the legs and open upon their basal joints.

The embryo emerges from the egg as a larva provided with a rostrum, and with three pairs of appendages, which represent the short anterior three pairs in the adult.* The four pairs of great limbs of the adult are produced by outgrowths from a subsequent posterior elongation of the body.

* A. Dohrn, 'Untersuchungen über Bau und Entwickelung der Arthropoden.' Erster Heft. 1870.

The comparison of the embryos of the *Pycnogonida* with those of the *Acarina*, especially such as leave the egg with three pairs of appendages, appears to me to leave little

Fig. 92.

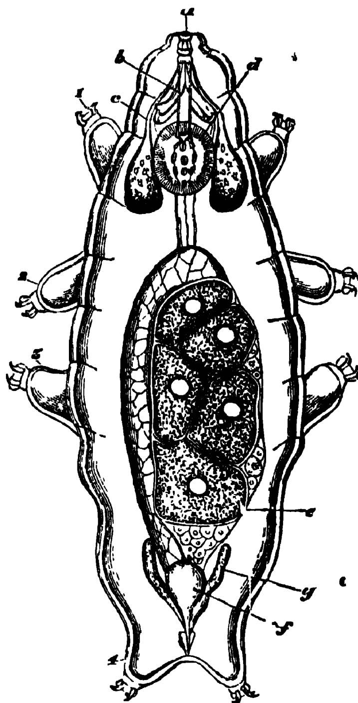


Fig. 92.—*Macrobiotus Schultzei* (× 100).—*a*. mouth with six oral papillæ; *b*, gullet, calcified stylets; *c*, salivary glands; *d*, muscular pharynx; *e*, ovary; *f*, vesicula seminalis; *g*, testis; 1, 2, 3, 4, limbs. (After Greeff.*)

doubt that the rostrum of the larval *Pycnogonum* is formed, as in the Mites, by the coalesced representatives of the

* "Untersuchungen über den Bau der Bärthierchen." ('Archiv für Mikr. Anat.' 1866.)

chelicerae and pedipalpi. If so, the seven other pairs of limbs are, by three pairs, in excess of the number found in any Arachnidan. On the other hand, the hexapod larva of the *Pycnogonida* differs from the hexapod *Nauplius* of the *Crustacea*, inasmuch as the three pairs of appendages of a *Nauplius* always represent antennary and mandibular appendages, and these, by the hypothesis, are to be sought in the rostrum of the *Pycnogonida*.

The fact to which reference has already been made, that the embryo Scorpion has six pairs of rudimentary appendages, attached to as many of the anterior free somites, of which one pair only remain (as the pectines) in the adult, leads me to suspect that the *Pycnogonida* may represent a much modified early Arachnidan form, from which the *Arthrogastra*, *Araneidea*, and *Acaridea* have branched off.

The ARCTISCA, or TARDIGRADA, are microscopic animals, found in association with *Rotifera*, in moss and in sand, rarely in water, which present many points of resemblance to the *Acarina*. The body (Fig. 92) is vermiform, with four pairs of tubercles representing limbs, terminated by two or more claws. The fourth pair is directed backwards at the hinder end of the body, so that if these appendages answer to the hinder pair of limbs in the typical *Arachnida*, the hinder thoracic, and all the abdominal, somites are undeveloped. The mouth is situated at the extremity of a rostrum provided with two stylets, which is so like that of the *Acarina*, that it may probably be regarded as formed by the coalescence of cheliceral and pedipalpal tubercles. There is a muscular pharynx, leading into a wide alimentary canal, which gradually narrows to the anus. No organs of circulation or of respiration exist. The paired ventral ganglia, which correspond in number with the appendages, are large. They are connected by longitudinal commissures with one another, and with a præ-œsophageal cerebral mass which sometimes bears two eyes. The *Arctisca* are hermaphrodite, the ovarian sac and the two testes opening together into a cloacal dilatation in

which the intestine terminates. The ova are relatively very large, and the cuticle of the parent is cast off and encloses them when they are laid, as a sort of ephippium. Complete yelk division takes place. The young have one-third the size of the adult when they are hatched, and they undergo no metamorphosis, beyond the addition, in some cases, of one pair of limbs after birth.*

The PENTASTOMIDA.—A still more aberrant form is the

Fig. 93.

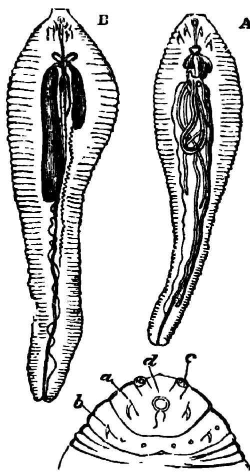


Fig. 93.—*Pentastomum tænioides.*—A, male; B, female; C, anterior end of the body; *a*, anterior hooks; *b*, posterior hooks; *d*, mouth; *c*, rudimentary palpiform organs. (After Leuckart)

parasitic *Linguatula*, or *Pentastomum*, which is found in a sexless condition in the lungs and liver of herbivorous mammals and of reptiles, and in the sexual state in the nasal cavities and maxillary antra of Carnivores. Thus, as Leuckart's investigations have proved, *Pentastomum*

* Kaufmann, "Entwickelung und systematische Stellung der Tardigraden." ('Zeit. Wiss. Zoologie,' 1851.)

tænioides, which inhabits the latter cavities in the Dog and the Wolf, is the sexual state of the *P. denticulatum*, which occurs in the liver of Hares and Rabbits.*

The *Pentastomida* are elongated vermiform animals, the bodies of which are divided by close-set transverse constrictions into numerous short segments. At first sight, they appear to be entirely devoid of appendages, but, on careful inspection, four curved hooks are found, two on each side of the mouth, which is situated rather behind the anterior extremity of the body. Each hook is solid, and its base projects into the cavity of the body and gives attachment to the muscular bands by which it is moved.

The mouth is surrounded by a chitinous ring; a narrow œsophagus leads from it into a nearly cylindrical, straight,

Fig. 94.



Fig. 94.—Embryo of *Pentastomum tænioides*.

alimentary canal, which terminates in the anus, in the middle line of the posterior extremity of the body. A mesentery is attached to the whole length of the alimentary canal and holds it in place. A nervous ring surrounds the œsophagus, and posteriorly presents a ganglionic enlargement whence nerves are given off to the body. The muscles are striated. The sexes are distinct, and the males are usually much smaller than the females.

The testicle is an elongated sac which lies on the ventral aspect of the intestine, and is connected anteriorly with two vasa deferentia. These terminate on the fore part of the ventral aspect of the body, each having a saccular

* 'Bau und Entwickelungsgeschichte der Pentastomen,' 1860.

dilatation which contains a very long, coiled, chitinous penis. In the female, the ovary is also a large sac and the oviducts come off from its anterior end, but the genital aperture is close to the anus.

The ova undergo their development in the ovary. The embryos are oval, but taper to the posterior end. In the middle line, in front, are three sharp protractile styles, of which the middle is the longest. Two pairs of articulated limbs are attached to the middle of the ventral aspect; each is terminated by a double hooked claw. The embryo of *Linguatula* thus resembles those of the *Acarina*, on the one hand, and those of such parasitic *Crustacea* as *Anchorella*, on the other.

In the case of *Pentastomum tænioides*, the embryos, enclosed in their vitelline membranes, pass out of the bodies of the dog or wolf, along with the nasal mucus. Taken into the body along with the food of the hare or rabbit, they emerge from the egg, penetrate the walls of the intestine, and lodge themselves in the liver. Here they become encysted, grow, and go through a series of changes of form, accompanied by repeated ecdyses, until they pass into the state known as *Pentastomum denticulatum*. If the flesh of the rodent containing *P. denticulatum* is devoured by a dog, the parasite passes into the frontal sinuses, or maxillary antra of the latter, gradually takes on the form of *P. tænioides*, and acquires sexual organs. The parasitism of the *Pentastomida*, therefore, is very similar to that of the *Cestoidea*.

Spiders and Mites abounded in the tertiary epoch, as their remains preserved in amber, show. Various *Arthrogastra* occur in the mesozoic formations, while Spiders and Scorpions of large size have been found in the carboniferous rocks.

The MYRIAPODA.—In these Arthropods, the body is divided into many segments, the most anterior of which takes on the characters of a distinct head; and almost all these segments bear articulated limbs terminated by claws. In the Centipedes (*Chilopoda*), the segments of the body have broad sterna, and the bases of the limbs are far apart;

but, in the Millipedes (*Chilognatha*), the sternal region is rudimentary, and the bases of the limbs are close together. Moreover, in the latter group, the majority of the segments of the body bear two pairs of limbs, and probably represent two somites.

Fig. 95.

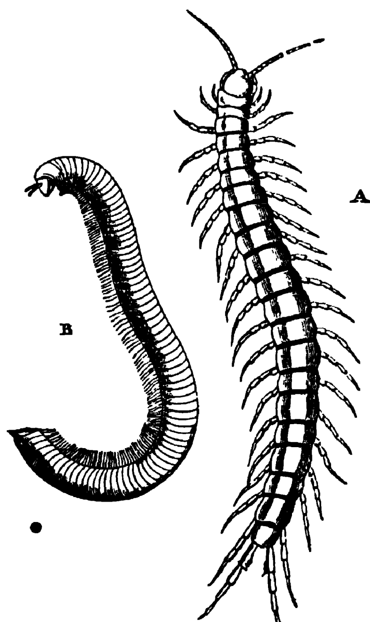


Fig. 95.—A, *Scolopendra borbonica* (*Chilopoda*). B, *Iulus flavozonatus* (*Chilognatha*).*

The head is either flattened from above downwards (*Chilopoda*), or from before backwards (*Chilognatha*). Some species are blind, but the majority have eyes, which are generally small and not very numerous ocelli, though, in

* 'Règne Animal.' Illustrated edition.

some cases, they are large compound eyes. There is always a pair of jointed antennæ.

The majority have the mouth constructed for biting, and are provided with a pair of mandibles, the most important peculiarity of which is that they are jointed, and thus depart less from the type of the ordinary limb than do

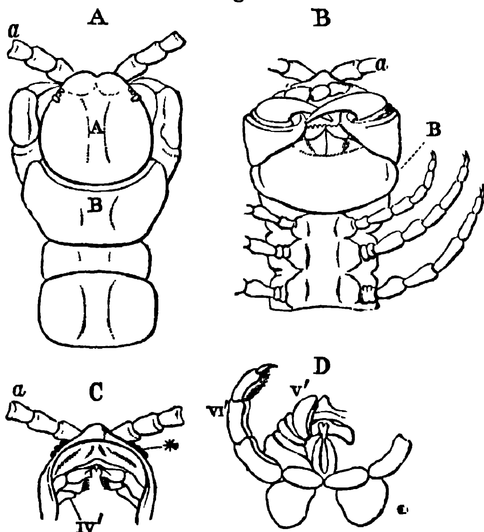


Fig. 96.—*Scolopendra Hopei* (after Newport).
A, dorsal view of the anterior part of the body. *a*. antennæ. A, cephalic segment; B, basilar segment.
B, ventral view of the head; *a*, B, as before.
C, under view of the cephalic segment, showing the antennæ, *a*; the eyes *; the labrum and the mandibles, IV'.
D, the second pair of gnathites V', and the first pair of appendages of the basilar segment VI'.

those of insects, while, to the same extent, they approach the gnathites of the *Peripatidea*. The mandibles are more modified in the *Chilopoda* (Fig. 96) than in the *Chilognatha*. In the latter, the second pair of gnathites form a broad four-lobed plate which plays the part of an underlip, while,

in the *Chilopoda*, they are soft and jointed, and united at their bases by a bilobed median process (Fig. 96, v′). In the *Chilognatha* the four segments which follow the head are free, and their appendages resemble ordinary limbs. The anterior pair is turned forwards and comes into relation with the mouth, and the tergum of the first somite is often enlarged; of the other three somites, the appendages of one appear to be always abortive. Thus there are three segments with single pairs of legs. The rest each bear two pairs.

In the *Chilopoda*, on the contrary, the head is followed by a *basilar segment* (Fig. 96, B), formed, according to Newport, by the union of four embryonic somites, and carrying three pairs of appendages. Of these the first are limb-like, but are turned forwards beneath the mouth (Fig. 96, D vi′); the second pair are the strong recurved poison-claws, and the hindermost pair may become functional legs, resembling those which are attached to the succeeding somites, but are always smaller than the others, and may be altogether aborted in the adult. The somites of the body never bear more than one pair of limbs.

The alimentary canal is usually straight and simple, like that of an insect larva. There are large salivary glands, and the intestine is provided with Malpighian tubules.

The heart extends through the greater part of the length of the body, and is many-chambered, there being one chamber for each of the somites in which it lies. Each chamber is somewhat conical in shape, being broader behind than in front, and admits the blood by a pair of lateral clefts, while the blood leaves it, in part, by the communication with the adjacent chamber, in part, by lateral arterial branches. A median aortic trunk continues the heart forwards, and the lateral trunks encircle the œsophagus and unite into an artery which lies upon the ganglionic chain. The arterial system in the *Chilopoda* is, in fact, as complete as that of the Scorpions.*

* Newport, "On the structure, relations and development of the nervous and circulatory systems in the Myriapoda and macrurous Arachnida." ('Philosophical Transactions,' 1863.)

The respiratory organs are tracheæ, which open by stigmata on the lateral or ventral surface of more or fewer of the somites. In *Scutigera* the stigmata are situated in the median dorsal line of the body.

The nervous system presents a ventral chain, with a pair of ganglionic enlargements for each segment of the body, the most anterior of which are connected by commissures, which embrace the œsophagus, with the cerebral ganglia.

The ovary in both *Chilognatha* and *Chilopoda* is long, single, and tubular in form. It lies above the alimentary canal in the latter, between the alimentary canal and the nervous system in the former. The double vaginæ open on, or close behind, the bases of the second pair of legs in the *Chilognatha*; at the posterior end of the body, beneath the anus, in the *Chilopoda*. Two spermathecæ and *colleterial* glands are very generally present.

The testes in the *Chilognatha* are tubular glands, which occupy the same position as the ovary and open in the same region. They have lateral cæca, and are connected by transverse ducts. Two copulatory organs, or penes, are developed on the sternal face of the sixth segment which follows the head, or are connected with the bases of the seventh pair of legs.

In the *Chilopoda* there is a good deal of variation in the structure of the testis. Thus in *Lithobius*,* the testis is a single filiform tube, connected at the hinder end with two deferent ducts which embrace the rectum. A large cæcum, apparently a vesicula seminalis, opens into each deferent duct. But, in most Chilopods, the testes are fusiform acini, united by delicate ducts with a median vas deferens. Two, or four, pairs of accessory glands are connected with the opening of the male apparatus.

The spermatozoa are enclosed in spermatophores in *Scolopendra*, *Cryptops*, and *Geophilus*.

The *Chilognatha* copulate. In *Glomeris* and *Polyxenus* the genital apertures of the two sexes are brought together

* Favre, "Anatomie des organes reproducteurs des Myriapodes." ('Annales des Sciences Naturelles,' 1855.)

during copulation; but, in *Iulus*, the penes of the male are charged with the spermatic fluid before copulation takes place, and it is by their agency that the female is impregnated.

The *Chilopoda* have not been observed to copulate, indeed the female shows a tendency to destroy the males, as among Spiders. The male *Geophilus* spins webs like those of spiders across the passages which he frequents, and deposits a spermatophore in the centre of each.

Metschnikoff * has recently shown that, in the *Chilognatha*, the process of yelk-division is complete, and confirms the observation of Newport (Phil. Trans. 1841) that the sternal face of the blastoderm becomes sharply infolded down its centre, in such a manner that the anterior and the posterior halves of that face of the embryo become closely applied together. Metschnikoff further points out that only two pairs of appendages are converted into gnathites; and that a chitinous cuticula, apparently identical with what Newport describes as the "amnion" in *Iulus*, is early thrown off from the embryo. In some species, it developes a median tooth-like process which serves to burst the vitelline membrane. Newport describes a short cord, or *funiculus*, which connects the anal extremity of the embryo with the so-called "amnion." It is not improbable that this is simply the continuation of the first larval skin into the rectum.

The embryo *Iulus* at first bursts the vitelline membrane, and is enclosed only in the embryonic integument. At this period, its body is divided into eight segments, of which the first represents the head. Traces of the antennæ are visible on the sides of the head, and the four following segments exhibit papillæ; those of the second, third and fifth segments develope into the three pairs of functional limbs, with which the young myriapod is at first provided.

Between the terminal segment and the seventh, the body grows and becomes divided into six rudimentary new

* "Embryologie der doppelfüssigen Myriapoden (*Chilognatha*)." ('Zeitschrift für Wiss Zoologie,' 1874.)

segments. The terminal segment also becomes divided into two. Thus, when the young escapes from the embryonic integument it consists of nine complete segments, including the head, with six rudimentary segments interposed between the penultimate and the antepenultimate—making fifteen in all; which is the full number of segments (head + three thoracic + eleven abdominal somites) possessed by an insect larva.

There is this difference, however, between the insect and the larval myriapod, that since, in the latter, there are only two pairs of gnathites, which must answer to the mandibles and first maxillæ of insects; the ambulatory appendages of the second segment must represent the second maxillæ of insects; and hence, though there is apparently the same number of somites in the two cases, there must in reality be one fewer in the myriapod. The myriapod larva therefore, notwithstanding its hexapod character, is essentially different from an insect larva.

The sixth and the seventh segments develope two pairs of legs, as do all the newly-formed segments; and it is worthy of notice that the male copulatory apparatus, inasmuch as it is situated in the seventh (sixth postcephalic) segment in the adult, is developed from one of the primary segments of the embryo, and not from the subsequently added segments. New segments, each giving rise to two pairs of limbs, are developed by sixes in the germinal region between the penultimate segment and the hindermost of the newly-formed segments, until the full number of the adult is complete.

In all other *Chilognatha* of which the development has been traced, the young, at first, possess only three pairs of functional legs; and one of the four segments which follow the head is apodal. According to Fabre, the apodal segment in *Polydesmus complanatus* is the second, and not, as in *Iulus*, the third.

In the *Chilopoda*, the young leave the egg with seven (*Lithobius*, *Scutigera*) or a greater number of pairs of ambulatory limbs. *Scolopendra* is said to be viviparous. The

early stages of development of *Geophilus* have been described by Metschnikoff.* Complete yelk-division takes place, and when the young leaves the egg it has a cylindrical body, like that of one of the *Chilognatha*, and possesses many pairs of limbs.* Newport† has pointed out that, in *Geophilus longicornis*, the basilar segment is formed by the confluence of four somites, of the appendages of which only two are ultimately developed. Thus the basilar segment of the head of the *Chilopoda* appears to correspond very closely with the four somites which follow the head in the *Chilognatha*. Under these circumstances, the difference in the position of the reproductive apertures in the two groups is exceedingly remarkable.

Fossil *Myriapoda* occur both in the tertiary and secondary formations, and there seems no reason to doubt that the *Xylobius sigillariæ* discovered in the coal of Nova Scotia by Lyell and Dawson is to be referred to this group.

The INSECTA.—Notwithstanding the vast number, and the singular diversity of form of Insects, the fundamental unity of their structure is remarkable, and, in this respect, the group exhibits a striking contrast to the *Crustacea*.

The division of the body into three regions, head, thorax and abdomen, is usually well marked, not only by the peculiar modifications which the cephalic and thoracic somites undergo, but by the attachment of the three pairs of ambulatory limbs exclusively to the latter. The head possesses four pairs of appendages, that is to say, one pair of antennæ and three pairs of gnathites; and, as a general rule, there is a pair of compound eyes, sessile upon the sides of the head; sometimes simple eyes are added to them. The first pair of gnathites are the *mandibles*, which are always devoid of a palp. The second pair are the *maxillæ*, which, in those insects in which the mouth is least modified, are distinct from one another and laterally moveable; while

* 'Zeitschrift für Wiss. Zoologie,' 1875.

† Monograph of the class Myriapoda, order Chilopoda. ('Transactions of the Linnean Society,' xix.)

the third pair of gnathites are united together in the median line, and constitute the *labium* of entomologists. In front of the oral aperture is a median plate, the *labrum*; while from the floor of the mouth formed by the labium another median process, the *lingua*, is usually developed.

It is hardly open to doubt that the mandibles, the maxillæ, and the labium, answer to the mandibles and the two pairs of maxillæ of the crustacean mouth. In this case, one pair of antennary organs found in the latter is wanting in insects, as in other air-breathing Arthropods, and the existence of the corresponding somite cannot be proved. But if it be supposed to be present, though without any appendage, and if the eyes be taken to represent the appendages of another somite, the insect head will contain six somites, the præoral sterna being bent up towards the tergal aspect, as in the higher *Crustacea*.

The three somites which succeed the head are termed respectively *prothorax*, *mesothorax*, and *metathorax*. A pair of legs is normally attached to each; and, when wings exist, they are lateral expansions of the tergal region (corresponding with the pleura of *Crustacea*) of the mesothorax or the metathorax, or of both.

In the abdomen there are, at most, eleven somites, none of which, in the adult, bear ambulatory limbs. Thus, assuming the existence of six somites in the head, the normal number of somites in the body of insects will be twenty, as in the higher *Crustacea* and *Arachnida*.*

One of the commonest of insects, the Cockroach (*Blatta* (*Periplaneta*) *orientalis*) is fortunately one of the oldest, least modified, and in many ways most instructive forms; at the same time, it is not too small for convenient dissection.†

In this insect, the head is vertically elongated, flattened

* It is open to question whether the podical plates represent a somite; and therefore it must be recollected that the total number of somites, the existence of which can be actually demonstrated in insects, is only seventeen, viz., four for the head, three for the thorax, and ten for the abdomen.

† See for an excellent figure and description, Rolleston, 'Forms of Animal Life,' p. 199, plate vi.

from before backwards, and connected by a distinct neck with the prothorax. The antennæ are slender, as long as, or rather longer than, the body. Large reniform compound eyes are situated at the sides of the head. The tergal portion of the prothorax (*pronotum*) is a wide shield, which overlaps the head, in front, and the tergal portion of the mesothorax, or *mesonotum*, behind. The legs are strong, and increase in length from the first pair to the last. The abdomen is flattened from above downwards, and bears a pair of elongated, many-jointed, setose styles (*cerci*) at its hinder extremity.

The males differ very considerably from the females. They have two pairs of wings, of which the anterior are brown, and are of a stiff and horny texture. As they serve to cover the posterior wings, they are termed *tegmina*. When closed, the left overlaps the right, and they extend back as far as the posterior edge of the tergum of the fifth abdominal somite.

The posterior wings, on the contrary, are thin and membranous; and, in a state of rest, are folded longitudinally upon themselves, the folded edge being internal. In this condition they are triangular, the base of the triangle lying close to the posterior edge of the fourth abdominal somite, and the right a little overlapping the left. When forcibly unfolded and made to stand out at right angles to the body, each of these wings is seen to have a nearly straight, thickened, anterior edge, while its rounded outer and posterior edges are very thin. The wing is strengthened by radiating thickenings, or *nervures*, united by delicate transverse ridges; and, when left to itself, it springs back into its folded state with some force.

The abdomen of the male is not very broad. The sterna of the abdominal somites are all flattened; and, to the hindermost, two minute unjointed styles are attached, while some singular hooked processes are seen, on close inspection, to protrude between the hindermost tergum and the hindermost sternum. The abdomen of the female is very much broader, especially towards the middle of its

length. The hindermost sternum is convex and boat-shaped, and its posterior half is separated along the middle line into two halves, united only by a thin and flexible membrane. Sometimes, the great egg-case, which the female carries about for some time before it is laid, is seen protruding between the posterior terga and sterna. The female has moveable tegmina, but they are very small, inasmuch as they do not extend beyond the middle of the metathorax, and are widely separated in the middle line; they are, in fact, mere rudiments of the anterior wings. The posterior wings appear, at first, to be altogether wanting. But the outer extremities of the *metanotum*, or tergal portion of the metathorax, present triangular areas, in which the integument is very thin and exhibits markings which simulate the nervures of the wings. There can be no doubt, in fact, that these are undeveloped wings, and they show, in a very instructive manner, that the wings are modifications of that part of the insect skeleton which answers to the pleura, and therefore to the lateral parts of the carapace, of a crustacean.

The convex dorsal wall of the head of the Cockroach (Fig. 97), is termed the *epicranium*. A median suture, the *epicranial suture*, may be seen, especially in young Cockroaches, traversing it from before backwards, and dividing between the eyes into two branches, one of which passes towards the articulation of each antenna. The basal joint of the antenna is attached to a transparent flexible membrane, which occupies an oval space, the antennary fossa, and allows of the free play of the antenna. A little projection of the hard chitinous skeleton when it bounds the inferior margin of the fossa, helps to support the joint. On the inner side of and above the antennary fossa, there is an oval fenestra, covered only by a thin and transparent portion of the integument, which allows a subjacent tissue of glistening white appearance to be seen (Fig. 97, I. II. *b*). These have been regarded as rudimentary ocelli by some entomologists; but their structure needs careful examination before this view can be adopted.

The transparent cornea of the eye, situated external to and behind the antennary fossa, is elongated, wider above

Fig. 97.

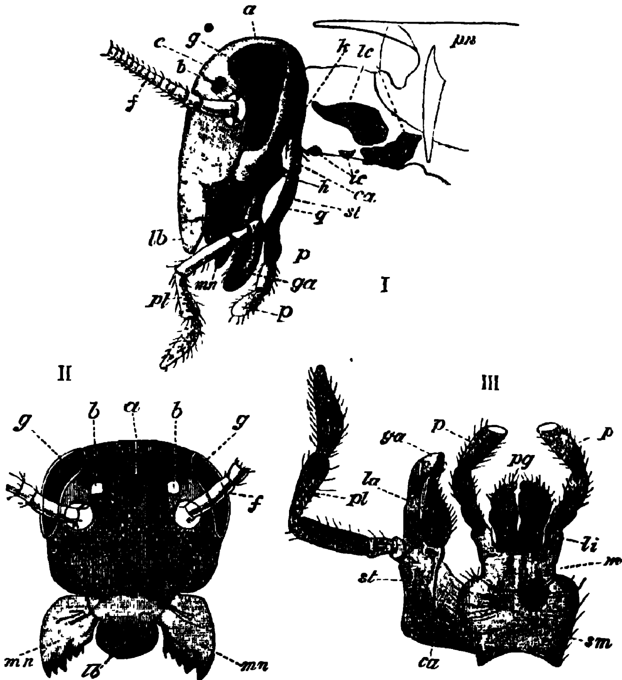


Fig. 97.—*Blatta orientalis.*—I II. side and front views of the head; *a*. the epicranial suture, at the ends of the lateral branches of which are *b*, the fenestræ; *f*, the antennæ; *g*, the eyes; *lb*, the labrum; *mn*, the mandible; *ca*, the cardo; *st*, the stipes; *ga*, the galea; *pl*, the palpus of the maxilla; *p*, the palpus, *q*, the mentum and submentum of the labium; *k*, the margins of the occipital foramen; *i*, *c*, inferior cervical sclerites; *lc*, lateral cervical sclerites; *p n*, pronotum. III. The labium and the right maxilla, viewed from below; letters as before except *la*, lacinia of the maxilla; *pg*, paraglossæ; *li*, ligula; *m*, mentum; *sm*, submentum of the labium.

than below, and has a concave anterior, and slightly convex

posterior margin. The numerous facets into which the cornea is divided, are hexagonal in shape, and very small.

The broad flattened region of the fore part of the head, on the oral side of the epicranial suture, is the *clypeus*. It is prolonged in front of the mouth, and with the truncated edge of this prolongation, the flap-like labrum is freely articulated. Behind the labrum are two, very stout, curved mandibles, strongly toothed at their extremities (Fig. 97, II. *m n*). Each mandible is articulated with the truncated edge of the lateral part of the skeleton of the head, beneath the eyes, which is termed the *gena*, in such a manner as to be freely moveable towards and from the median line, but in no other direction. The proximal end of the maxilla (Fig. 97, III.) is formed by an elongated basal articulation, the *cardo*, which is directed transversely to the axis of the head, and is connected with the inferior margin of the epicranium, or rather with a thin skeletal band which runs round the posterior margin of the epicranium, and is firmly united with it only on its dorsal side. This band forms the boundary of the so-called *occipital foramen*, by which the cavity of the head communicates with that of the neck, the chitinous wall of the latter region being continuous with it. Articulated at right angles with the cardo is the *stipes*, or second joint of the maxilla. This is freely moveable in the lateral direction, and its outer distal angle bears the continuation of the limb, or *palpus*, formed by two short and three long joints. Two processes terminate the stipes; of these the anterior and outer, the *galea*, is soft, rounded and possibly sensory in function, while the posterior and inner—the *lacinia*—is a curved cutting blade with a toothed and spinose inner edge.

The labium (Fig. 97, III.) consists of two incompletely separated median plates, the *submentum* behind, and the *mentum* in front; upon the latter follows a bilobed terminal piece, the *ligula*, each lobe of which is again divided longitudinally into two portions, which have considerable similarity to the galea and lacinia of the maxilla. The outer is usually termed the *paraglossa*.

Between the mentum and the ligula, on each outer edge of the labium, a small piece, the *palpiger*, is articulated; it bears the three-jointed *labial palpus*, which is to be regarded as the proper free termination of the second maxilla. The resemblance between the labium and a pair of maxillæ which have coalesced, is obvious.

The submentum is not directly articulated with the cranial skeleton, but its posterior edge is close to one of the *cervical sclerites*,* or skeletal elements observable in the chitinous integument of the neck, of which there are altogether seven. One is dorsal, median, and marked by a deep longitudinal depression. It articulates with the dorsal margin of the occipital foramen. Four are lateral, two on each side (Fig. 97, I. *lc*); these take an oblique course from the dorsal part of the boundary of the occipital foramen, with a tubercle of which the anterior piece is articulated, to the anterior edge of the episternum of the prothorax. The inferior cervical sclerites (Fig. 97, I. *ic*) are two narrow transverse plates, one behind the other in the middle line. They appear to represent the part called *gula*, which in many insects is a large plate, confluent with the epicranium above and supporting the submentum anteriorly. I think it is probable that these cervical sclerites represent the hindermost of the cephalic somites, while the band with which the maxillæ are united, and the genæ, are all that is left of the sides and roof of the first maxillary and the mandibular somites; the epicranial expansions being mainly formed by the upward and backward extension of the ophthalmic and antennary sterna, which arise out of the procephalic lobes of the embryo. In addition to these externally visible sclerites, there is a sort of internal skeleton (*endocranium* or *tentorium*), which extends as a cruciform partition from the inner face of the lateral walls of the cranium, close to the articulation of the mandible, to the sides of the occipital

* I use this term, in the sense in which it has been employed by Milne-Edwards, to denote any definite hardened part of the chitinous skeleton. It is to the latter what a distinct ossification is to the skeleton of a vertebrated animal.

foramen. The centre of the cross is perforated by a rounded aperture, through which the œsophageal nerve-commissures pass. The commencement of the œsophagus traverses the interspace between the anterior processes of the cross; the tendons of the great adductors of the mandible pass through the lateral apertures; and the backward continuation of the gullet enters the thorax through the posterior aperture, included between the tentorium and the margins of the occipital foramen.

In each somite of the thorax, a distinct median sclerite, the *sternum*, may be observed; and a much larger tergal piece, the *notum*. At the sides of the somite are other definitely arranged sclerites, the anterior of which appear to answer to the episternum and epimera in the *Crustacea*, while the posterior, perhaps, properly belong to the attached limb.

Forked or double apodemes, the *antefurca*, *medifurca*, and *postfurca*, project from the sternal wall of each somite of the thorax into its cavity. They support the nervous cord and give attachment to muscles.

The legs present a large basal joint, the *coxa*, between which and the third, termed *femur*, a small articulation, the *trochanter*, is interposed. Upon the femur follows an elongated *tibia*; and this is succeeded by the *tarsus*, which consists of six joints. Of these, the proximal joint is long and stout, the three next are short, the fifth is elongated and slender; the sixth, very short, is terminated by two curved and pointed claws (*ungues*).*

The broad differences in the structure of the abdomen of the male and female have been already pointed out. Of the eight terga externally visible in the female (Fig. 98), the first is shorter than those which succeed it; and the hindermost (Fig. 98, 10) is escutcheon-shaped, deflexed

* Mr. Westwood ('Modern Classification of Insects,' vol i. p. 416) says that the tarsi are five-jointed, and that there is a pulvillus between the ungues. The sixth joint appears to be what Mr. Westwood terms *pulvillus*, but it is a true joint provided with a special flexor, the slender tendon of which, however, traverses several of the joints of the tarsus.

at the sides, thin in the middle, and notched at the end. When this tergum is gently pulled backwards, two other very narrow terga (Fig. 98, 8, 9), of which the anterior overlaps the posterior, and which were hidden between it and the antepenultimate or seventh tergum become visible. The apparent eighth tergum is therefore really the tenth. Beneath the tenth tergum are two triangular *podical* plates (Fig. 98, 11), one on each side of the anus. Provisionally, I take them to be the sclerites of the eleventh abdominal somite.

The first sternum is confluent with the second, and largely hidden by the coxæ of the metathoracic limbs. The seventh is greatly enlarged, and its posterior edge is produced into a boat-shaped process, nearly divided into two portions by an inward fold of the integument along the median line.

Completely hidden by the seventh sternum is a thin plate, narrower in front than behind, where it is produced on each side. Anteriorly, it is articulated with the sternum of the following somite, so as to form a sort of spring-joint, which ordinarily keeps it applied against the latter, and therefore directed obliquely upwards and a little forwards. The large aperture of the vulva (Fig. 98, *v*) lies in the middle of this plate. On the sternal region behind the vulva, between it and the anus, arises a pair of elongated processes, divided into two portions, of which the outer is thick and soft, the inner slender, pointed, and hard. They embrace and partly ensheath two other processes having somewhat the shape of knife blades, the anterior fixed ends of which are curved, and, being attached to the sides of the somite to which they belong, are distant, while the blades meet, and are applied together in the middle line. Of these, which may be termed *gonapophyses*, the study of their development shows that the posterior bifid pair belong to the ninth somite, while the anterior pair belong to the eighth.

The cerci (*x*) are attached to the dorso-lateral part of the tenth somite.

In the abdomen of the male *Blatta* (Fig. 99), the ten terga are readily discernible; but the eighth and ninth are

very short, and the former overlaps the latter. The tenth tergum is flat, and has a freely projecting, truncated, posterior margin. Articulated beneath its lateral edge are two multiarticulate cerci (*x*), similar to those of the female.

Beneath the tenth tergum, and hidden by it, are the two podical plates (11) between which the anus opens. The first sternum is small, and may easily escape notice. The second to the sixth sterna are of nearly equal width and length. The seventh and eighth are narrower; the ninth still narrower and longer, about half of its length being covered by the eighth. The covered half is different in texture from the uncovered, being thinner and more transparent, and its anterior margin is deeply notched. The uncovered half is strong, horny and dark-coloured, convex below and concave above; its free posterior margin is obscurely trilobed by two lateral shallow notches. On each side, a slender, unjointed, setose style, which projects backwards and outwards, is attached to this sternum.

Thus the tergal surface of the abdomen of the male essentially resembles that of the female, while the sternal surface differs in exhibiting two sterna more (namely, the eighth and ninth) without dissection. Hence, while, in the female, the opening of the recto-genital chamber lies between the tenth tergum and the seventh sternum, in the male it lies between the tenth tergum and the ninth sternum.

When the tenth tergum and the podical plates are removed, a very singular apparatus, the male genital armature, comes into view. It consists of a number of chitinous processes having the form of plates and hooks, the exact form and disposition of which could be made intelligible only by numerous figures. It may be stated generally, however, that these plates and hooks terminate processes of the sternal region of the tenth somite, on each side of the aperture of the vas deferens, and therefore, though they are of the same nature as the gonapophyses of the female, they are not their exact homologues.

The most conspicuous division of the right gonapophysis

Fig. 98.

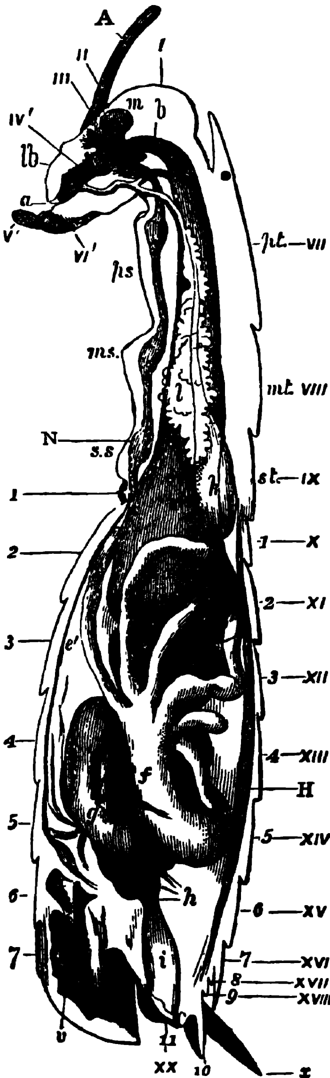


Fig. 98.—Longitudinal and vertical section of a female Cockroach (*Blatta*).—I to XX, somites of the body; 1 to 11, somites of the abdomen; A, antenna; *lb*, labrum; *a*, mouth; *b*, œsophagus; *c*, crop; *d*, proventriculus; *e*, pyloric cæca; *f*, chylific ventricle; *g*, insertion of the Malpighian cæca; *h*, intestine; *i*, rectum; *v*, vulva; *l*, salivary gland; *k*, salivary receptacle. By an error the duct is made to terminate above instead of beneath the lingua; H, position of heart; *m*, cerebral ganglia; N, thoracic ganglia; *x*, cerci.

is a broad plate divided at the extremity into two portions, the inner of which curves inwards and ends in two or three sharp spines, while the outer is coiled upon itself so as to resemble a short corkscrew. The left gonapophysis is pro-

Fig. 99.

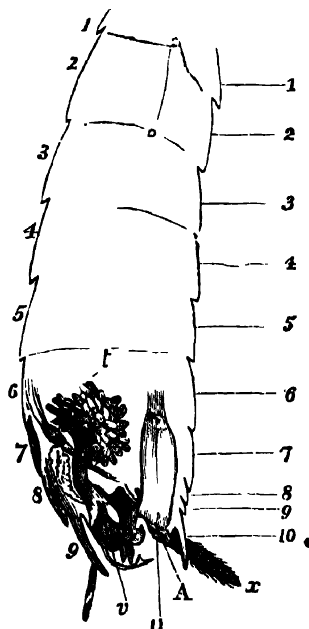


Fig 99.—Longitudinal and vertical section of the abdomen of a male Cockroach (*Blatta*).—1, 2, 3, 4, &c., terga and sterna of the abdomen; *t*, mushroom-shaped gland; *v*, aperture of the vas deferens; A, anus.

vided with a long process like a tenaculum, the incurved extremity of which is denticulated.

The alimentary canal of the Cockroach commences by the oral cavity, situated between the labrum in front, the

mandibles and maxillæ at the sides, and the labium, with the large *lingua*, or *hypopharynx*, behind. The œsophagus, beginning as a narrow tube, passes between the anterior crura of the tentorium, and then leaving the head by the occipital foramen and traversing the neck and thorax, gradually widens into the large crop or *ingluvies* (Fig. 98, *c*), which lies in the abdomen. This is followed by the small thick-walled *proventriculus* (Fig. 98, *d*), shaped like a pear, with its broad end applied against the crop. The narrow end of the proventriculus opens into a wide canal, the so-called *chylific ventricle*, or *ventriculus* (Fig. 98, *f*), an elongated tube, the junction of which with the intestine, is marked by the insertion of the numerous Malpighian tubes. The anterior end of the ventriculus is provided with seven or eight cæcal diverticula of unequal lengths (Fig. 98, *e*), the *pyloric cæca*. The first portion of the intestine (*ileum*) is narrow. The next, termed the *colon*, is very wide, and somewhat sacculated. A constriction marks off the region of the colon from the straight short *rectum* (Fig. 98, *i*), which terminates in the anus, situated at the hinder extremity of the body between the podical plates.*

The aperture by which the mouth communicates with the gullet is small, and situated at the superior and anterior part of the buccal cavity. A broad projection of the

* M. F. Plateau ('Recherches sur les phénomènes de la digestion chez les Insectes,' 1874; 'Note sur les phénomènes de la digestion chez la Blatta américaine [*Periplaneta americana*],' 1876; and 'Recherches sur les phénomènes de la digestion chez les Myriapodes,' 1876), divides the alimentary canal of insects and myriapods into a buccal, a median, and a terminal portion. The buccal portion consists of the œsophagus, crop, and proventriculus—which last he considers to be a mere strainer and to have no masticatory function. The middle division lies between the proventriculus and the insertion of the Malpighian tubes. The terminal division extends from the latter point to the anus. With the solitary exception of *Iulus*, the secretions of the alimentary canal are always alkaline, and that which effects the transformation of the albuminoid elements of the food into peptones appears to be furnished by the middle division, which is lined by epithelium, devoid of any cuticle. In carnivorous insects digestion may take place in the crop by the flow of the secretion of the middle intestine into it. The salivary fluid of *Blatta* rapidly effects the transformation of starch into sugar.

posterior and inferior wall of the buccal cavity occupies all the space between the œsophageal opening of that cavity and the labium, and ends in a free subcylindrical process. This is termed *hypopharynx* or *lingua*, but it might be well to reserve the term *lingua* for the free end, and *hypopharynx* for the attached posterior portion. The anterior surface of the hypopharynx slopes downwards and forwards; its sides are supported by two sclerites, which are narrow and rod-like above and broad below, where they unite in an arch on the dorsal face, just where the free part, or lingua, begins. On the under side of the lingua are two broader sclerites, which also unite and form an arch, which lies over the opening of the salivary duct. The anterior surface of the lingua and hypopharynx is beset with fine hairs.

The two salivary glands, with their receptacles, are greatly developed in the Cockroach.* The glands (Fig. 98, *l*) lie on each side of the œsophagus and crop, extending through the thorax, as far as the commencement of the abdomen. Each gland is a white mass, as much as a quarter of an inch long and composed of numerous acini. The ducts which arise from these acini unite first into a single trunk on each side, and then, beneath the sub-œsophageal ganglion, the two trunks join to form the single short salivary duct which opens beneath the lingua. The ducts of the salivary glands are lined by a transversely ribbed chitinous membrane, so that they greatly resemble tracheæ.

The salivary receptacles (Fig. 98, *k*) are elongated oval sacs, three-eighths of an inch long, each of which is situated at the extremity of a long duct. The ducts unite in front with one another, and with the duct of the gland, to form the short terminal common duct. The receptacle and its ducts have a chitinous lining similar to that of the duct of the glands, but the spiral marking does not extend over the walls of the receptacle.

The proventriculus has a thick muscular coat, and the

* The salivary glands are well described by Basch, "Untersuchungen über die chylopoietische und uropoietische System der Blatta orientalis." ('Sitzb. Wiener Akad.,' 1858.)

chitinous lining which is continued into it from the ingluvies is greatly thickened and produced into six hard, brown ridge-like principal teeth. Posterior to these is a circle of six prominent cushions covered with setæ, and similar setæ beset the lining membrane of the funnel-shaped cavity into which they project. Between each pair of principal teeth are five smaller tooth-like ridges, of which the median is the largest, and a variable number of still finer longitudinal elevations lie between them.

The proventriculus leads posteriorly into a narrow, thick-coated canal, the tubular extremity of which projects freely into the much wider anterior end of the chylific ventricle, and constitutes a very efficient valve.

The short and narrow anterior division of the intestine (*ileum*) is separated from the colon by a circular valve, the surface of which is beset with small spines.

The Malpighian glands are very numerous (20–30), delicate, cæcal tubules, of even diameter throughout, and lined by a small-celled epithelium enclosing a central cavity.

The communication between the colon and the rectum is very narrow, but is not valvular. The walls of the rectum itself are raised into six ridges, which project into its interior and are abundantly supplied with tracheæ; these are the so-called *rectal glands*. Anal glands appear to be absent.

The histology of the alimentary canal has been particularly studied by Basch.* From the oral cavity to the funnel-shaped extremity of the proventriculus, it is lined by a chitinous coat continuous with the chitinous layer of the integument, and beset for the greater part of its extent with fine setiform processes. Beneath this is the proper endoderm, consisting of a layer of cells. Next follows a structureless membrana propria or basement membrane; and this is succeeded by two layers of striped muscular fibres, the internal disposed longitudinally, and the external circularly. In the proventriculus, the muscular

* 'Sitzungsberichte der Wiener Akademie,' xxxiii., 1858.

layers become much thicker, and some of those of the outer layer acquire a radial arrangement, while the longitudinal muscles are disposed in bundles which correspond with the six principal ridges. In the chylific ventricle, the muscular layers and the basement membrane are disposed much as before. The basement membrane presents pits on its free surface in which rounded cells are lodged, and is beset between these by the elongated cells of a cylinder epithelium. The free ends of these present a thick wall, marked by vertical striations. There is no chitinous layer. The cæca are merely diverticula of the wall of the chylific ventricle.

The intestine, finally, repeats the structure found in that part of the alimentary canal which lies in front of the chylific ventricle and is provided with a setose chitinous lining.

Basch found the secretion of the salivary glands and the contents of the crop acid,* and that an infusion of the salivary glands, acidulated with hydrochloric acid, digested fibrin. The contents of the chylific ventricle were neutral or alkaline; and an infusion of the chylific ventricle at once turned starch into sugar. The same effect was produced by an infusion of the salivary glands.

The heart (Fig. 98, *h*) is a slender inconspicuous tube, which occupies the middle line of the dorsal wall of the abdomen and presents, at intervals, pairs of lateral apertures. The wall of the abdomen internal to the chitinous integument is lined by a soft cellular substance (*hypodermis*), the outer layer of which represents the ectoderm or epidermis, while the deeper part is the parietal layer of the mesoderm. This last contains a stratum of longitudinal muscular fibres, divided into segments or *myotomes*, in correspondence with the somites, and numerous tracheæ. The heart is enclosed in the abdominal wall which surrounds it on all sides, leaving only a small pericardial space.† Beyond the slender aortic

* Plateau denies that the salivary secretion of *Blatta* is ever acid, and ascribes the occasional acidity of the contents of the crop to the food.

† Cornelius ('Beiträge zur näheren Kenntniss von *Periplaneta* (*Blatta*) *orientalis*,' 1853), found that the pulsations of the heart could readily be observed

canal in which the heart terminates anteriorly, and which passes into the thorax and the head, no vessels appear to be given off from the heart.

Delicate triangular sheets of muscular fibre, the *alary muscles*, are attached in pairs by their bases to the wall of the pericardial chamber, while their apices are inserted into the hypodermis. They occupy the interspaces left by the principal dorsal branches of the tracheæ, which form arches on each side of the heart.

From the inner face of the abdominal wall, processes are given off, some of which appear to hang freely into the abdominal cavity, while others accompany the numerous tracheæ which pass to the alimentary canal. When the abdominal cavity is laid open, its inner lining has a villous appearance and often seems to be full of free granular matter, as the processes very readily break up into fragments. The substance which thus fills up the interspace between the parietes of the abdomen and the contained organs is the *corpus adiposum*. It is made up of cells often so arranged as to form a network, and it usually has a milk-white colour, which arises partly from the air contained in the tracheæ, and partly from innumerable, strongly refracting granules contained in its component cells.

There are ten *stigmata* on each side of the body of *Blatta*, eight in the abdomen, and two in the thorax. The latter are situated between the prothorax and the mesothorax, the mesothorax and the metathorax, respectively; above the attachment of the coxæ and beneath the terga. The abdominal stigmata lie in the soft integument which connects the sterna and terga of the somites. All the stigmata are situated in conical thickened elevations of the integument. The thoracic stigmata are the largest, and the anterior pair have a distinctly two-lipped aperture, the anterior lip being notched in the centre. The openings of the abdominal

in *Blattæ* which had recently undergone ecdysis. They were as frequent as eighty in the minute; but allowance must be made for the disturbed condition of the insects under observation.

stigmata are more oval and are inclined backwards. Immediately within each stigma the tracheal trunk into which it opens is provided with a valvular arrangement, by which the passage can be closed or opened.

Fig. 100.

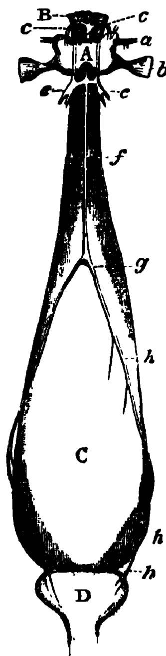


Fig. 100.—*Blatta orientalis.*—A, the brain with the antennary (*a*) and optic (*b*) nerves; *c*, *e*, *f*, *g*, *h*, stomato-gastric nerves; B, the anterior end of the gullet; C, the crop; D, the gizzard.

The large tracheæ which take their origin from these stigmata immediately divide and give off dorsal and ventral branches; the former unite in a series of arches on each side of the heart, while, on the ventral side, the branches

are connected by trunks which run parallel with the abdominal ganglia. Large tracheæ pass from the anterior thoracic stigma through the neck into the head and, in the abdomen, the viscera receive an abundant supply of air-tubes.

The lobes of the corpus adiposum are also plentifully supplied with tracheæ, while fine trunks enter the substance of the ganglia and nerves and there ramify. Tracheæ accompany the nervures of the wings and are abundantly distributed to the muscles.

The nervous system consists of the supra-œsophageal ganglia (Fig. 100, A), commonly termed the brain, united by thick and short commissures with an infra-œsophageal ganglionic mass, situated in the head; of three pairs of large coalesced ganglia in the thorax, one for the prothorax, one for the mesothorax, and one for the metathorax; of six pairs of closely united smaller ganglia in the abdomen; and of a set of visceral or *stomato-gastric nerves.* The several pairs of thoracic and abdominal ganglia are united by double commissural cords. In the males the commissures which unite the abdominal ganglia are not straight, but are bent, as if it were needful to make allowance for the possible elongation of the abdomen. The supra-œsophageal ganglia give off the nerves to the antennæ from their antero-lateral angles; while their postero-lateral angles are produced into the great optic nerves. Above the margin of each antennary nerve there is a small rounded tubercle which is in immediate relation with the silvery patch which shines through the fenestra on the inner side of the antennary fossa. Beneath this tubercle, and on the inner side of the antennary nerve, arises the root of the stomato-gastric system of nerves. Each root passes forwards for a short distance, then turns inwards, and in the middle line, enters a heart-shaped ganglion situated on the gullet (Fig. 100, *c*). From this a median cord passes backwards beneath the brain and enters a ganglion, which is connected on each side with two others (*e*, *e*). The continuation of the median cord passes back

along the tergal wall of the œsophagus, and where this begins to dilate into the crop ends in a small triangular ganglion (*g*), whence lateral branches are given off, which can be traced as far as the gizzard.

The exact form and arrangement of the male organ of generation has only recently been made out. The most conspicuous of these organs is a mushroom-shaped gland (Fig. 99, *t*) composed of a great number of short cæca attached to the extremity of the also very short vas deferens. It is lodged in the hinder end of the abdomen, and covers the posterior abdominal ganglion. The contents of the cæca are viscid, granular, and usually brilliantly white. The anterior end of the vas deferens is dilated, and the cæca are arranged in two groups which open into each side of the dilatation. The contents of the vas deferens are also white and viscid, and evidently consist in great measure of the secretion of the cæca. In the adult male, however, innumerable spermatozoa with straight rod-like heads, and long flagella are to be found intermingled with the contents of the vas deferens and its dilatation. On the sternal side of the mushroom-shaped gland, between it and the last abdominal ganglion, there is an accessory gland composed of dichotomous monilated tubes, lined by a columnar epithelium, all bound together by a common investment into a flattened elongated mass.

As the duct of the mushroom-shaped gland in the adult male always contains spermatozoa, and no other organ containing spermatozoa is to be found, this gland has naturally been taken for the testis. Rajewsky,* however, has recently pointed out that the true testes are situated in the tergal region of the abdomen, and that they may be found in this region in the young and yet wingless males, though they are much obscured by the corpus adiposum which invests them. He traces the efferent duct of the testis to the glands just mentioned. In the adult male the testes atrophy, and are hardly to be discovered among the masses

* Hofmann and Schwalbe, 'Jahresbericht,' 1875. The original paper is in Russian, and I have not seen it.

of the corpus adiposum. I have found the testes in the young males in the position assigned to them by Rajewsky. They consist of numerous oval or pyriform sacs attached by short pedicles to a common duct.

The *ovaries* (Fig. 101) are two groups of eight tubes, situated on each side of the hinder half of the abdomen. The ovarian tubes, or *ovarioles*, of each group communicate with a short oviduct, which soon unites with its fellow in the

Fig. 101.

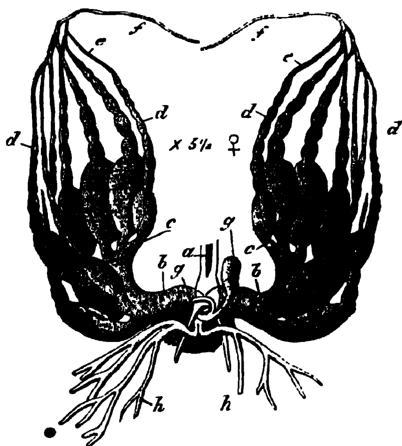


Fig. 101.—*Blatta orientalis* —Female genital organs : *a*, the posterior abdominal ganglion ; *b*, the oviducts ; *c*, *d*, *e*, the ovarian tubes ; *f*, the filament by which their extremities are united ; *g*, the spermatheca ; *h*, the colleterial glands.

middle line and opens externally by the very short and wide vagina. The finely tapering anterior ends of the ovarioles of each side are continued forwards by delicate cellular prolongations. These finally unite together into one long filament, which can be traced for some distance forwards among the lobes of the corpus adiposum. It is a cellular cord, which appears to be nothing but a process

of the mesoderm. Numerous nucleated cells, from some of which the ova take their origin, while others remain as interstitial cells, which are eventually converted into an epithelium, make up the substance of the slender anterior terminations of the ovarioles. The ova situated behind these enlarge, and become disposed in a single series. Further on, the epithelial cells form a thick stratum round each egg, and possibly assist in the formation of the large vitellus with which it is ultimately provided. As the egg advances towards maturity, the vitellus acquires first a finely, and then a coarsely granular structure, and the germinal vesicle and spot, previously conspicuous, are no longer to be seen. Behind the junction of the oviducts with the vagina, and the last abdominal ganglion which lies upon the latter, there is a small sac with a long neck from which a short cæcal process is given off. It has a thick chitinous lining and a muscular investment, and is the *spermatheca*. Behind it are two, large, ramified, tubular *colleterial glands*, which probably give rise to the substance of which the egg case is formed. Their conjoined ducts open behind the spermatheca.

The eggs are enclosed, sixteen together, in strong capsules of a horny consistency, shaped somewhat like a cigar case, and presenting a longitudinal slit, the raised and serrated edges of which are closely applied to one another. It is through this slit that the fully developed young make their exit. The eggs attain $\frac{1}{6}$ of an inch in length. Each has its own thin but tough brownish shell, the surface of which is beautifully ornamented with hexagonal patches of minute tubercles. They are arranged parallel with one another in two opposite series, one series occupying each half of the case. The eggs, adapting themselves to the form of the case, are convex outwards and concave inwards, and thus, though their ends touch, a median space is left between the two sets. The inner concave face of the egg is that on which the sternal face of the embryo is situated. The female carries the egg-case about for a week or more, before depositing it. The young leave the eggs as minute active

insects, colourless, except for the large dark eyes. Before they are hatched they acquire eyes, antennæ, gnathites, legs, and short cerci, which differ only in detail from those of the perfect *Blatta*, into which the larva passes by successive ecdyses. According to Cornelius (*l. c.* p. 29), the Cockroach undergoes seven ecdyses; the first immediately on leaving the egg, the second, a month later. After the second ecdysis, the insect sheds its skin only once a year; so that it attains its adult condition only in its fifth summer. The chitinous cuticula splits along the median line of the tergal aspect of the head, thorax and abdomen, before it is cast.

Thus the Cockroach is said to be an insect without metamorphosis. For although the male, in the later stages of its growth, acquires wings, and thus does become very sensibly metamorphosed from a merely cursorial animal to one which has, at any rate, the capacity for flight, there is no period in the life of this insect in which the larva passes into a resting condition, during which it takes no food, and in the course of which it developes its wings. In other words, the Cockroach passes through no *pupa* state, which the insect enters as a larva, and leaves as an imago, such as is so well known to occur in the course of the development of Moths and Butterflies. The term *metamorphosis*, in its technical entomological sense, is applied only to that succession of changes of which such a definite pupal condition forms the middle term.

It is obvious that a metamorphosis, in this sense, is a secondary complication superinduced upon the direct and gradual process of development exhibited by such insects as the Cockroach;* and that the *Metabola*, as insects having a metamorphosis are termed, are, so far, more differentiated than the *Ametabola*, or those which have no metamorphosis. Again, in each of these divisions, it is clear that the insects which never possess wings are less differentiated, or more

* Sir John Lubbock has shown that the young *Chloëon* (*Ephemera*) *dimidiatum* undergoes more than twenty ecdyses, each accompanied by a slight change of form in its passage to the adult state. (Trans. Linn. Soc. 1863.)

embryonic, than those which are winged. And finally. insects with the parts of the mouth in the condition of ordinary gnathites are less differentiated than those in which such gnathites are changed in form and function, or become confluent.

The insects which, in this view of their morphological

Fig. 102.

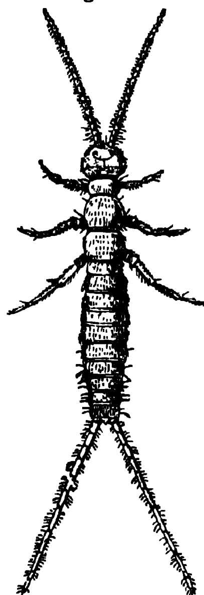


Fig. 102.—*Campodea staphylinus*, one of the *Thysanura* (after Lubbock).*

relations, occupy the lowest position in the group, are the *Collembola* and *Thysanura*, the *Mallophaga*, and the *Pediculina*, inasmuch as they possess no trace of wings and undergo no metamorphosis.

The *Collembola* and *Thysanura* undergo no metamor-

* 'Monograph on the *Collembola* and *Thysanura*,' pl. liii.

phosis, and are always wingless. The abdomen contains six segments only in the *Collembola* (*Podura*, *Smynthurus*, *Tomoceros*), in which group the mouth is usually provided with mandibles and maxillæ, though these, instead of being articulated with the sides of the head, are capable of being retracted into its interior.* In the genus *Anoma* the mouth is suctorial.

The *Thysanura* (*Lepisma*, *Campodea*, *Japyx*) resemble the young *Blattæ*. They have ten well-marked abdominal somites (*Campodea*, Fig. 102), and the gnathites conform to the mandibulate type. The abdomen in *Machetes* has a pair of elongated cylindrical appendages attached to every segment except the first; while *Campodea* and *Japyx* have seven pairs of such abdominal appendages.†

The *Collembola* are provided with a curious tube or sucker, which is attached to the sternum of the first abdominal somite, and gives exit to a glandular process, which secretes a viscid matter. Most of the insects belonging to this group possess a curiously contrived "spring and catch" attached to the sternal region of the penultimate or antepenultimate somites of the abdomen, by the help of which they execute their vigorous leaps.

Sir John Lubbock could find no trace of tracheæ in any of the *Collembola* except *Smynthurus*, though they are easily seen in many of the *Thysanura*. According to the same authority *Lepisma* has four Malpighian tubes, while *Campodea*, *Japyx*, and many *Collembola* have none.

The *Mallophaga* are parasites upon mammals and birds, on the hairs and feathers of which they feed. The head and body are depressed, the eyes simple, the gnathites of the masticatory type. The abdomen has nine or ten visible segments.

The *Pediculina*, or Lice, subsist upon the blood of the mammals on which they are parasites. The gnathites are

* Lubbock 'Monograph on the *Collembola* and *Thysanura*,' p. 37.

† The myriapod *Scolopendrilla* has similar appendages attached to each segment along with legs. (Lubbock, *l.c.*)

converted into a piercing and sucking apparatus. The under side of the head presents a soft protrusible proboscis, provided externally with minute horny hooks, and traversed by a canal which leads into the œsophagus. The proboscis incloses two grooved chitinous styles which are applied together by their concave sides; and, within the sheath thus formed, lie two finely-pointed chitinous setæ which can be moved up and down in the sheath.*

The proboscis is, in all probability, formed by the union

Fig. 103.

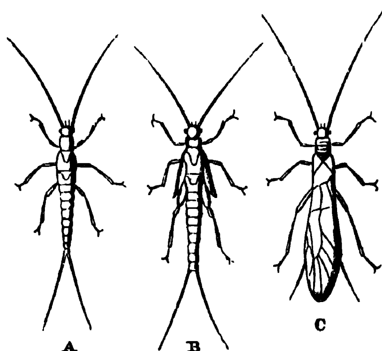


Fig. 103.—*Perla nigra.*—A, the aquatic apterous larva. B, one of the transitional stages between this and the perfect insect C. ('Règne Animal.')

of the labrum with the second pair of maxillæ, while the two halves of the horny sheath are the mandibles, and the setæ, the first maxillæ. The prothorax, mesothorax, and metathorax are hardly distinguishable, and the abdomen has nine visible segments.

The *Orthoptera* (Fig. 103) and the *Hemiptera* (Fig. 104) are ametabolous. The majority have two pairs of similar or more or less dissimilar wings in the adult state, and

* Gerstfeldt, 'Ueber die Mundtheile der Saugenden Insecten,' 1853.

in the apterous forms it is probable that the wings are aborted, not typically absent. In the *Orthoptera** (the Termites, Cockroaches, Grasshoppers, Crickets, Day-flies, Dragon-flies and Earwigs), the mouth is constructed upon the same plan as that of *Blatta;* but the *Physopoda* or *Thysanoptera* (*Thrips* and its allies), small winged insects which live chiefly in flowers, present a modification which is transitional to the Hemipteran mouth (Gerstfeldt, *l. c.*). There is a proboscis directed backwards and formed by the union of the labrum with the labium, which last is provided with palps, though they are sometimes very small. The

Fig. 104.

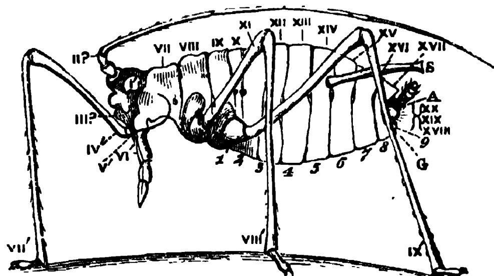


Fig. 104.—*Aphis pelargonii.* Apterous agamogenetic form.

maxillæ are palpigerous and are united at their bases with the labium. The mandibles are styliform setæ enclosed in the proboscis.

In the *Hemiptera,*† all of which suck the blood of animals or the juices of plants (Bugs, Plant-lice, *Cicadæ*), wings may be present or absent, and the eyes are usually compound. The visible abdominal somites may be reduced to six. The gnathites are modified to form a piercing and suctorial apparatus, which is similar, in many respects,

* The *Thysanura* and the *Physopoda* are often united with the *Orthoptera* in modern classifications, while the *Ephemeridæ* and *Libellulidæ* used to be arranged with the *Neuroptera.*

† The *Mallophaga* and the *Pediculina* are united with the *Hemiptera* by some authors.

to that of the *Pediculina.* There is a usually sharp and pointed labrum, while the mandibles and maxillæ are mere tubercles, surmounted by long chitinous pointed styles, of which therefore there are four. The labium is usually represented by a median, jointed, fleshy, elongated body, the anterior face of which presents a longitudinal groove in which the mandibles and maxillæ are enclosed. Neither the maxillæ nor the labium are provided with palps.

Thus, in the series of ametabolous insects there are some with masticatory, others with suctorial mouths. It is by no means clear that the gnathites of the suctorial mouth of the *Hemiptera* are to be regarded as modifications of

Fig 105.

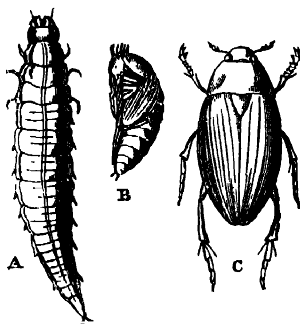


Fig. 105.—*Hydrophilus piceus.*—A, larva. B, pupa. C, imago. ('Règne Animal.')

masticatory gnathites of the type exhibited by the *Orthoptera.* The absence of palps is a very significant fact, suggesting that the Hemipteran mouth is the extreme term of a series of modifications for the commencement of which we must go back to the *Myriapoda.*

The metabolous *Coleoptera,* or Beetles (Fig. 105), have masticatory mouths of the same general type as those of the *Orthoptera;* with which they are closely connected through the Earwigs. The two constituents of the labium are however much more completely confluent than in the *Orthoptera.*

There are usually two pairs of wings, the anterior pair being converted into stiff horny elytra; these take no part in the act of flight, but serve as covers to the metathoracic wings, which, in the state of rest, are folded up beneath them. The number of apparent somites of the abdomen is often much reduced. In the metabolous *Neuroptera* (Ant-lions, Caddis-flies, Scorpion-flies), in some of which the insect is more or less active during the pupa state, the parts of the mouth are, for the most part, very similar to those of the *Orthoptera*. In two groups of *Neuroptera*, however, the mouth becomes suctorial. Thus in the *Trichoptera*, or Caddis-flies, the labrum is elongated and grooved posteriorly; the mandibles are aborted, the bases of all the gnathites are united. and the labrum is a spoon-shaped body. In the Scorpion-flies (*Panorpina*), there is, according to Gerstfeldt, a proboscis formed in front by the elongated clypeus and labrum, and behind by the coalesced maxillæ. The mandibles are small, and the first maxillæ much elongated. The ordinary four palps are present.

The *Neuroptera* have two pairs of wings of a delicate reticulated structure. The metathoracic wings may or may not be folded.

What appears to be a further development of this type of mouth is found in the *Lepidoptera* (Butterflies and Moths). The labrum and the mandibles abort, and the labium is represented only by a triangular plate which bears two large palps. On the other hand, the maxillæ, the palps of which are always very small, are often immensely elongated and applied together by their channelled inner faces, thus constituting a sucking proboscis (Fig. 106, 107). The wings, similar in character, and covered with minute scales, are rarely absent. Both pairs are used in flight.

In the metabolous *Diptera* (Flies and Fleas, Fig. 108), the mouth is constructed upon the same plan as that of the *Hemiptera*, so far as the conversion of the labium into an organ of suction is concerned; but usually the metamorphosis of the gnathites is carried still further, and the maxillæ have palps. Thus in the Fleas, which are parasitic on mammals and

birds, what appears to be the labrum is an elongated, slender style, which lies between the two elongated mandibles. The first maxillæ are broad triangular plates, each with a four-jointed palp. The second maxillæ (labium) are represented by a short median lamella, which bounds the

Fig. 106.

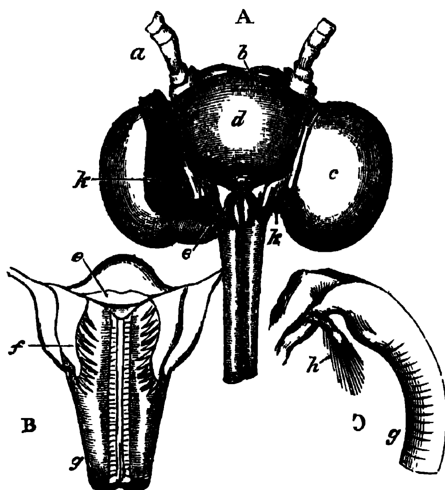


Fig. 106.—The head, A, and parts of the mouth, B, C, of *Sphinx ligustri*.—*a*, antenna; *b*, epicranium; *c*, cornea; *d*, clypeus posterior; *e*, labrum; *f*, mandible; *g*, maxilla; *h*, maxillary palpus; *k*, labial palpus. B, base of the maxillæ with the mandibles and labrum; C, lateral view of the same. (After Newport.)

Fig. 107.

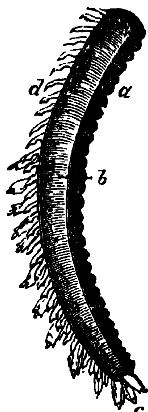


Fig. 107.—*Vanessa atalanta*.—Inner or concave surface of the apical portion of the right maxilla; *a*, transverse muscles; *b*, canal; *c*, papillæ; *d*, hooks which join the maxillæ.

mouth behind and is provided with two, long palps, which resemble knife blades and are imperfectly divided into four joints. The three somites of the thorax are distinct, and the two hinder ones have lamellar appendages, which possibly represent wings. The abdomen has ten somites.*

* See L. Landois, 'Anatomie des Hundeflohes,' 1866.

In those dipterous insects which are termed *Pupipara*, which are apterous, or nearly so, and parasitic upon mammals, birds and bees, a circular wall, or short proboscis, invests the other parts of the mouth. There are, first, two lateral, protrusible, horny plates; secondly, an anterior and a posterior seta; the latter stronger and grooved longitudinally in front. Between these is a single fine seta. Gerstfeldt considers that the last answers to the hypopharynx; the second pair, to the labrum and the second maxillæ; the first pair, to the first maxillæ; and that there are no mandibles.

The ordinary *Diptera*, which possess one pair of functional wings attached to the mesothorax, resemble the *Hemiptera* in possessing a usually fleshy proboscis, often tumid at its

Fig. 108.



Fig. 108.—*Syrphus ribesii.*—A, larva. B, pupa. C, imago. ('Règne Animal.')

extremity, which is formed by the confluent second maxillæ. As in *Hemiptera* also, the labrum is a more or less elongated pointed plate, and the mandibles and maxillæ are usually terminated by chitinous cutting setæ (Fig. 109). But the bases of these parts are constantly united together; there is a pair of maxillary palpi, and often a median, more or less styliform structure, usually considered to be the hypopharynx. It seems doubtful, however, whether this may not be formed by the coalesced terminations of the maxillæ. In the common House-fly, the labrum, mandibles, and maxillæ coalesce at their origins to constitute the base of the proboscis, which is mainly formed by the confluent second maxillæ. Its longitudinal grooved anterior face is overhung by the

elongated styliform labrum. The gnathites here exhibit almost the extreme modification of the piercing and sucking type of mouth.

Finally, the metabolous *Hymenoptera* with, usually, two pairs of reticulated scaleless wings present a series of modifications from the essentially masticatory mouth of the Ants to the partly masticatory and partly suctorial,

Fig. 109.

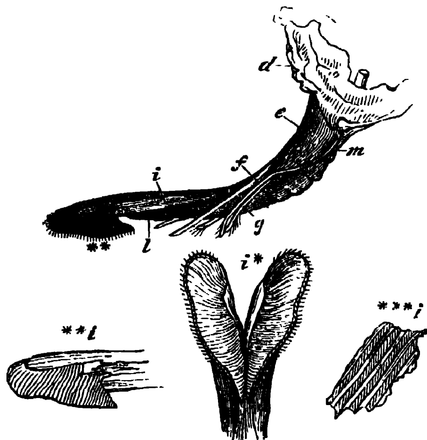


Fig. 109.—*Eristalis floreus*.—*d*, front of the head; *e*, labrum; *f*, mandible; *g*, maxilla and palpus; *i*, labium; *i** extremity of the labium separately and more magnified; *i***, inner surface of the paraglossæ; *i****, the rows of hairs on the inner surface; *l*, the ligula; *m*, the cardo and submentum. (After Newport.)

or rather, lapping mouth, such as is met with in the Bees. In the latter (Fig. 110) the labrum is small; beneath it, a median fleshy lobe—the *epipharynx*—overhangs the minute aperture of the mouth. The mandibles are strong with wide, almost spoon-shaped, extremities. The part of the maxilla which appears to answer to the *lacinia* in *Blatta*, is shaped like a knife-blade and folds upon the stout *stipes*, like a clasp-knife in its handle.

The short and almost rudimentary palp is attached to the extremity of the stipes. The *cardines* are long and

Fig. 110.

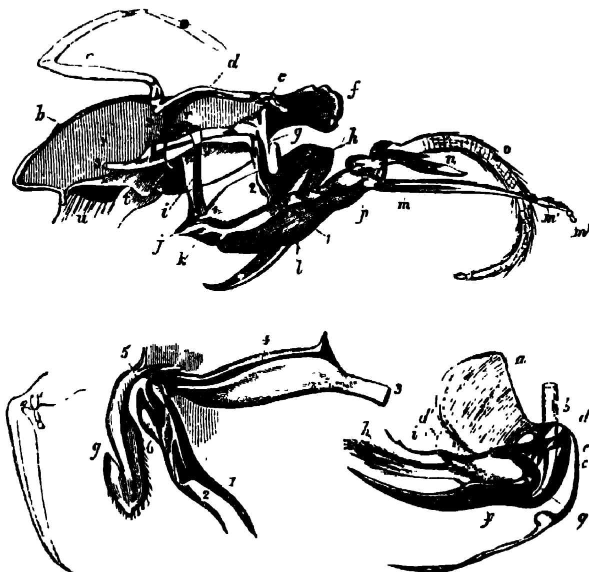


Fig. 110.—(Upper figure.) Section of the head of *Bombus*. *b*, ocellus; *c*, antenna; *d*, clypeus; *e*, labrum; *f*, mandible; *g*, epipharynx; *h*, maxilla; *i*, cardo; *j*, *k*, *l*, submentum and mentum; *m*, *m'*, labial palpus; *n*, paraglossa; *o*, lingua or median process of the ligula; *u*, occipital foramen; 1, 2, sclerites of the hypopharynx.
(Left lower figure.) Terminal portion of a maxilla.
(Middle lower figure.) Epipharynx and hypopharynx magnified; 1, 2, sclerites of the hypopharynx; 3, cut end of the œsophagus; 4, 5, sclerites in the wall of the œsophagus and sides of the mouth; 6, lip-like projection of the hypopharynx; *g*, epipharynx.
(Right lower figure.) *a*, Quadrate sclerite connected by a triangular piece with *c*, one of the lances of the sting; *b*, duct of the poison gland; *f*, grooved median piece in which the lances play; *h*, one of the lateral setose palpiform sheath-pieces; *g*, genital aperture.

slender and give rise to a hinge joint, whereby the maxillæ and labium can be folded back, like a carriage

step, under the head. The mentum is large, the labial palps long and slender; there are two large paraglossæ and, between them, a median, annulated, setose, cylindrical organ proceeds, which either represents the lingua, or is an independent prolongation of the ligula. Functionally, this organ is a tongue, and enables the bee to lap up the honey on which it feeds. The mandibles and maxillæ are employed as cutting and modelling implements, but appear to have little or nothing to do with mastication, properly so called.

The gnathites and the mouth are abortive in some insects, as the Day-flies, which take no food in the adult condition. The development of the different divisions of the alimentary canal varies greatly. Salivary glands are very generally present. In many suctorial insects, the ingluvies is a sac opening by a long duct into the gullet; a distinct proventriculus, provided with chitinous ridges, may be present or absent. The ventriculus appears to be always devoid of an inner cuticula. It may be devoid of cæca or beset with short cæca throughout its whole extent. The number of the Malpighian tubes, which are sometimes branched, varies from two to a multitude. In many cases they have been found to contain uric acid; but no biliary matter has yet been proved to exist in them. Anal glands are frequently appended to the termination of the rectum, and may secrete an acrid or stinking fluid.

In some larvæ (*Myrmecoleo, Dytiscus*) there is no proper median oral aperture, but canals which open on the extremities of the mandibles lead into the œsophagus. The alimentary canal has no posterior opening in the larvæ of many *Hymenoptera,* of *Myrmecoleo* and of the *Pupipara.* The salivary glands secrete the silken material in which the larvæ of the *Lepidoptera* invest themselves; while, in *Myrmecoleo* and the *Hemerobidæ,* it is the rectum which furnishes the silk.

The poison of the *Hymenoptera* is a fluid strongly impregnated with formic acid, which is secreted by a special

gland and poured into a reservoir connected with the sting.

In many winged insects both pairs of wings are developed and take equal shares in flight (*Hymenoptera, Lepidoptera, Neuroptera*). In the *Coleoptera*, the anterior pair are converted into horny wing-covers (*elytra*), and the posterior pair, much larger than the anterior and folded up under them when the insect is at rest, subserve flight. In the *Diptera* the posterior wings are represented only by short processes, the *halteres*. In the *Strepsiptera*, on the other hand, it is the anterior pair of wings which abort. In all orders of winged insects, individual cases of complete abortion of the wings occur either in the female alone, or in both sexes.

The posterior abdominal somites often undergo extensive modifications; they may be small and retracted within the anterior somites, or they may even become more or less completely abortive. In many insects, processes of the somites in the genital region of the female, which answer to the gonapophyses of *Blatta*, are converted into organs which assist in the deposition of the eggs and are termed *ovipositors*. The saws of the Saw-flies and the stings of other *Hymenoptera* are to be regarded as specially modified ovipositors. The laborious and thoughtful investigations of Lacaze-Duthiers * led him to the conclusion that all these organs are constructed upon the same plan; that they are developed from that somite of the abdomen which lies immediately behind the opening of the vulva; that this opening is always situated between the eighth and the ninth somite; and is therefore separated by three somites (the ninth, tenth, and eleventh), from the anus.

According to Lacaze-Duthiers, in those insects which are provided with an ovipositor, saw or sting, the ninth somite always consists of a single median tergal sclerite, to the inferior angles of which are connected two small more or less triangular pieces, each of which carries a long styli-

* "Recherches sur l'armure génitale femelle des Insectes." ('Annales des Sciences Naturelles,' 1849–1853.)

form appendage. There is a single median sclerite, which is the most important part of the boring apparatus; two small sclerites are united with the lateral angles of this piece, and there are two other elongated sclerites which constitute a valvular sheath. Thus, according to Lacaze-Duthiers' view, in the sting of *Bombus* (Fig. 94) *h* is one of the elongated lateral sternal sclerites, which with its fellow forms a sheath for the rest of the apparatus; *f* is the median sternal sclerite; it is pointed and grooved on its sternal surface; while *c*, one of the lances, is a process of the tergal half of the somite. Each lance is sharp and slender, and its tergal edge fits upon the margin of the groove of the median style, in such a manner as to be able to slide backwards and forwards upon it. The sternal edges of the two lances meet in the middle line, and, together with the median sternal piece, enclose a canal which serves to convey the secretion of the poison gland into the wound made by the sting. In the operation of stinging, the median piece serves as a sort of "director" for the two lances.

However, recent investigations into the development of stings and ovipositors,* *e.g.* the sting of the Hive-bee, and of the Wasp and the ovipositor of an Ichneumon-fly (*Cryptus migrator*), show that while the median grooved piece and the two sheath-pieces arise from papillæ developed upon the sternal surface of the ninth abdominal somite of the larva, the lances are the result of the metamorphosis of papillæ seated on the sternal surface of the eighth somite; and these papillæ are so similar to those from which the limbs are developed, that it becomes (to say the least) probable, that they represent true appendages of the somites to which they are attached, rather than mere modifications of the sclerites of the body-wall, as Lacaze-Duthiers supposed

* Kraepelin, "Untersuchungen über den Bau, Mechanismus und Entwickelungsgeschichte des Stachels der Bienenartigen Thiere" ('Zeitschrift für Wiss. Zoologie,' 1873); and Dewitz, "Ueber Bau und Entwickelung des Stachels und der Legescheide." ('Zeitschrift für Wiss. Zoologie,' 1875.) See also the observations of Packard, 'On the development and position of the Hymenoptera,' 1866.

them to be. In like manner, the examination of the development of the ovipositor of *Locusta viridissima* has proved that, of the three pieces of which each half of it is composed, two are developed from the sternum of the ninth and one from that of the eighth somite. But the two median pieces of the ninth somite do not unite together to form a single piece grooved below, as in the hymenopterous sting or ovipositor. And observations which I have made on the development of the gonapophyses of *Blatta*, lead me to the conclusion that the posterior bifid pair are developed from the ninth, and the anterior curved pair from the eighth somite. In this case the latter will be the homologue of the lances of the Bee sting.

Thus it would appear that, while there can be no doubt as to the general unity of plan of ovipositors and stings, the view of Lacaze-Duthiers must be modified. It must be admitted that these apparatuses appertain to the eighth and ninth somites, and not to the ninth alone; and that there is much reason to suspect that their chief constituent parts are modified limbs.

The male copulatory organs * are often very complicated, and their homologies have not yet been fully determined. Kraepelin (*l. c.*) who has examined the development of these parts in the Drone, and the modifications found in hermaphrodite Bees, is led to the conclusion that they are developed from the eighth and ninth somites of the abdomen, and therefore are the homologues of the parts of the sting in the female. In the male *Blatta*, however, it is obvious that the male copulatory apparatus belongs to a more posterior somite than that upon which the female gonapophyses are developed.

The heart usually has the form of a flattened tube, closed at its posterior end, but, in front, continued into the aorta,

* The male *Libellulidæ* possess a peculiar copulatory apparatus developed upon the sternum of the second abdominal somite. The genital aperture has the ordinary position, and hence, before copulation, the male has to bend the extremity of his abdomen upwards in order to load this apparatus with spermatozoa.

which may be traced as far as the cerebral ganglia, and appears to give off no branches. The sides of the tube present slit-like openings (*ostia*), which vary in number from two to nine pairs; and, when there are several pairs, each pair answers to a somite of the abdomen. The margins of the ostia may be simple, or may be produced inwards into folds which play the part of valves. Muscular or ligamentous fibres may extend from the hypodermis to the dorsal aspect of the heart, and serve to suspend it in place.

The alary muscles, which in most insects are fan-shaped, and lie in pairs, opposite one another, on each side of the heart, either unite in the middle line, or are inserted into a sort of fascia, on the sternal aspect of the heart, to which organ they are not directly attached.

The septum between the pericardial cavity and the general cavity of the abdomen thus formed, is termed by Graber * the *pericardial septum*. From their anatomical relations, therefore, the alary muscles can have nothing to do with the diastole of the heart, the pulsations of which indeed, go on just as well when the alary muscles are cut through. Graber throws out the very probable suggestion that the contraction of the alary muscles causes the pericardial septum to move towards the axis of the body, and by thus enlarging the cavity of the pericardium, facilitates the flow of blood to the ostia of the heart. The same investigator ascribes a special respiratory function to the abundant tracheæ which are distributed to the walls of the pericardium, and which, undoubtedly, must tend to facilitate the aeration of the returning blood.

In many insects, a septum, provided with transverse muscles, overlies the abdominal nerve-cord and separates a ventral blood sinus, in which the cord lies, from the abdominal cavity. The sinus is open in front and, as the muscles of the septum contract rhythmically from before

* "Ueber den propulsationischen Apparat der Insecten" ('Zeitschrift für Wiss. Zoologie,' 1873), and "Ueber den pulsirenden Bauchsinus der Insecten." (Ibid., 1876.)

backwards, they tend to drive the blood which enters it to the posterior end of the body.

In the respiratory system of insects the number of stigmata is observed to vary from one to ten pairs. As a rule, none are found in the head,* or between the head and the first thoracic somite, and they are usually absent from the terminal somites of the abdomen. A very common number is nine pairs; the first being situated between the mesothorax and the metathorax, and the rest between the following somites. Only two pairs of stigmata are found in the *Libellulidæ* and *Ephemeridæ*, and they are seated upon the thorax. In *Nepa* and *Ranatra*, there is only one pair of abdominal stigmata, in addition to those in the thorax, and in the larvæ of *Tipulidæ* and of *Hydrophilus*, the stigmata are reduced to one terminal abdominal pair. The stigmatic openings are usually situated upon the sides of the abdomen, but in some *Coleoptera* (e. g. *Dytiscus*) they are dorsal, and in many *Hemiptera* they are situated on the ventral aspect of that region of the body. Either the lips of the stigmatic aperture itself, or the walls of the tracheal trunk which arises from it, are so disposed as to constitute an occlusor apparatus, provided with a muscle, by the contraction of which communication with the external air can be cut off. This occlusor apparatus, long ago described in certain insects by Strauss-Durckheim, Newport, Burmeister, Siebold and others, has recently been specially investigated by Landois and Thelen,† who describe it as usually consisting of four essential parts: the *bow* (Verschluss-bugel), the *lip* (Verschluss-band), the *lever* (Verschluss-hebel), and the muscle. The bow is a thickening of one-half of the circumference of the chitinous lining. The lip is formed by the other half of the circumference, and the lever is a chitinous process connected with one end of the bow, or with the lip. When the lever is single, the muscle which is attached to it passes over the lip

* Sir John Lubbock found the two spiracles of *Smynthurus*, to be situated on the under side of the head, immediately below the antennæ.

† "Der Stigmenverschluss bei den Insecten." ('Zeitschrift für Wissenschaftliche Zoologie,' 1867.)

and is inserted into the opposite end of the bow. When it contracts, it therefore presses the lip against the bow. When two levers are present, they are attached to opposite ends of the lip and bow, and the muscle extends between their extremities. The effect of its contraction is to thrust the free edge of the lip against the bow.

The tracheal trunk which arises from a stigma may ramify without communicating with the rest; but, usually, the tracheæ which proceed from each stigma enter into more or less extensive anastomoses. Very commonly the main trunks of each side give off wide anastomotic branches, which unite and form a longitudinal trunk on each side of the body, while transverse trunks often connect the main tracheæ of opposite sides.

In many insects, especially those which possess great powers of flight, more or fewer of the tracheæ become dilated into sacs, in which the spiral marking of the chitinous lining is interrupted or disappears. In Bees and Flies, a vast air-sac is thus developed, on each side of the abdomen, from the longitudinal anastomotic trunk.

The aquatic larvæ of many *Orthoptera* (*Ephemeridæ*, *Agrion*, *Calopteryx*) and *Neuroptera*, and of some *Diptera*, *Lepidoptera*, and *Coleoptera*, though provided with a fully-developed tracheal system, possess no stigmata. The somites of the abdomen or of the thorax are, however, provided with delicate foliaceous or filamentous processes, into which branches of the tracheæ enter and ramify. The air contained in these tracheæ is therefore separated from that dissolved in the water only by a very thin layer of integumentary tissue, and an exchange of gaseous constituents between the two readily takes place. These are often called *branchiæ*, but they are obviously of a totally different nature from true branchiæ. The larvæ of some Dragon-flies (*Libellula* and *Æschna*) present yet another form of respiratory organ. Although they possess a pair of thoracic stigmata, these appear to have little or no functional importance, but respiration is effected by pumping water into and out of the rectum. The walls of the

latter are produced into six double series of lamellæ, in the interior of which tracheæ are abundantly distributed, and which play the same part as the tracheal branchiæ just mentioned. These rectal respiratory organs, in fact, appear to be a complicated form of the so-called "rectal glands" which are so generally met with in insects.

The chief agent of the movements of expiration and inspiration in insects is the abdomen, the capacity of which may be diminished by the approximation of its terga and sterna, and the shortening of its length by the retraction of its posterior into its anterior somites; while it may be enlarged by movements in the opposite directions. When the cavity is enlarged, air rushes in at the stigmata, and when it is diminished, if the stigmata are open, expiration occurs; but, if the stigmata are shut, the effect of the expiratory act must be to drive the air into the ultimate ramifications of the tracheæ. The movements of inspiration and expiration vary in rapidity with the condition of the insect. In the Bee, Newport observed that in the state of rest they were as few as forty, but that they rose to one hundred and twenty with muscular exertion.

The air-sacs doubtless assist flight by the diminution of the specific gravity of the insect, which follows upon their distention.

The sounds produced by insects * are, in a great proportion of cases, effected by the friction of hard parts of the integument one against the other. Thus the Grasshopper rubs the femur of the hind leg against a ridge on the anterior wing, and the chirp of the Crickets and Locusts is produced by the friction of the elytra. The parts which thus rub together are provided with serrations and ridges, which have a constant and characteristic disposition. The longicorn Beetles produce a sound by the friction of the tergum of the prothorax upon a process of that of the mesothorax, and the Dung-beetles by rubbing the coxæ of the hind legs against the hinder edge of the third abdominal sternum.

* See Landois, "Die Ton- und Stimm-Apparate der Insecten." ('Zeitschrift für Wiss. Zoologie,' 1867.)

Further, sounds are necessarily produced by the extremely rapid vibration of the wings, which characterises the flight of many insects. Landois, however, found that the thorax of a Bluebottle fly continued to buzz after the separation of the head, the wings, the legs, and the abdomen. The separation of the halteres weakened the sound but slightly. The acoustic apparatus, in fact, lies in the immediate neighbourhood of the thoracic stigmata. The main trunk of the tracheæ dilates into a hemispherical sac, which opens externally by the stigmatic orifice. The sac presents a hooplike thickening, to which are attached free chitinous folds or processes, and it is to the vibration of these that Landois ascribes the sound. The vocal organ of the Fly would thus appear to be a modification of the occlusor apparatus of the stigmata, just as the organ of voice of mammals is a modification of the occlusor apparatus of their respiratory opening.

In the *Cicadæ* the vocal organs are, according to Landois, the posterior thoracic stigmata. These open into chambers, in the walls of which tense membranes are so disposed as to intensify the sound by their resonance.

As in the *Crustacea*, so in insects, the central nervous system varies very much in the extent to which its component ganglia are united together. In most *Orthoptera* and *Neuroptera* and in many *Coleoptera*, the thoracic and abdominal ganglia remain distinct and are united by double commissures as in *Blatta*. In the *Lepidoptera*, the thoracic ganglia have coalesced into two masses united by double commissures; while in the abdomen there are five ganglia, with single or partially separated commissural cords. The concentration goes furthest in some *Diptera* and in the *Strepsiptera*, in which the thoracic and abdominal ganglia are fused into a common mass.

A system of stomato-gastric nerves similar in its general arrangement to that of *Blatta*, is very generally present.

A special system of nerves, termed *respiratory* or *transverse*, is found in very many insects, both in the larval and in the perfect condition. The principal nerves of this system are

arranged in pairs on the sternal aspect of the body, and their outer extremities anastomose with branches of the ordinary peripheral nerves and are distributed to the muscles of the stigmata. Their inner ends unite into a plexus, which lies over the interval between two of the ganglia of the central nervous cord, and they are connected by longitudinal cords with one another, and with these ganglia.

In insects, as in other arthropods, the branches of the nerves which are distributed to the integument, and especially those which pass to the bases of the larger or smaller setæ with which the integument is provided, frequently end in minute ganglia. Hensen has shown that in the *Crustacea*, similar setæ in all probability have an auditory function; and Leydig, Hicks, Lespès, Landois, and others, have ascribed functions of special sensation to these structures in insects. But whether these setæ, on the antennæ or elsewhere, subserve either hearing or smell, is still very doubtful; and the only organs which can safely be regarded as auditory in insects, are those which occur in Grasshoppers (*Acrididæ*), Crickets (*Achetidæ*), and Locusts (*Locustidæ*), and which were first accurately described by Von Siebold.* Recently, they have been studied by Leydig, Hensen, Ranke,† and Oscar Schmidt,‡ but it must be confessed that much obscurity still hangs over their minute structure.

In the *Acrididæ*, the chitinous cuticula of the metathorax presents on each side, above the articulation of the last pair of legs, a thin tympaniform membranous space surrounded by a raised rim. On its inner face, the cuticular layer of the tympaniform membrane is produced into two processes, one of which is a slender stem ending in a hollow triangular dilatation. A large tracheal vesicle lies over the tympanic membrane, and between its wall and the latter, a nerve derived from the metathoracic ganglion, passes to the region occupied by the processes, and there enlarges into

* 'Archiv für Naturgeschichte,' 1864.

† "Beiträge zu der Lehre von den Uebergangs-Sinnesorganen." ('Zeitschrift für Wiss. Zoologie,' 1875.)

‡ Schmidt, "Die Oehrorgane der Heuschrecken." ('Archiv für Mikr. Anatomie,' 1875.)

a ganglion, the outer face of which, beset with numerous glassy rods arranged side by side, is in contact with the tympaniform membrane. A nerve arising from this ganglion passes along a groove to the 'stem' and ends in a ganglion in its dilatation. From this ganglion certain fine filaments proceed.

In the *Achetidæ* and *Locustidæ*, the tibiæ of the fore legs present similar tympaniform membranes which are easily seen in the common Cricket, but, in other forms, become hidden by the development over them of folds of the cuticle of the adjacent region of the limb. Two spacious tracheal sacs occupy the greater part of the cavity of the tibia, and a large nerve ends in a ganglion in the remaining space. Upon this ganglion a series of peculiar short rod-like bodies are set.

The compound eyes of insects differ only in detail from those of the *Crustacea.*

In the *ocelli*, or so-called simple eyes, a sclerotic, a cornea, a lens, a vitreous humour, and a choroid coat, have been distinguished, and the whole organ has been compared to the vertebrate eye. But the 'lens' appears to be always a mere thickening of the cuticle which constitutes the cornea, and the so-called 'vitreous humour' is partially or wholly made up of crystalline cones analogous to those which are found in the compound eye. In this respect the ocellus of the insect resembles the simple eye in *Arachnida* and *Crustacea.**

Many insects, as the Glow-worm and Lantern-flies, are remarkable for their power of emitting light.

According to Schulze † the males of *Lampyris splendidula* possess two photogenic organs, which lie on the sternal aspects of the penultimate and antepenultimate abdominal

* Leydig, 'Das Auge der Gliederthiere,' 1864. Landois, "Die Raupenauge" ('Zeitschrift für Wiss. Zoologie,' 1866), and "Zur Entwickelungsgeschichte der facettirten Augen von *Tenebris molitor*" (Ibid., 1867).

† "Zur Kenntniss der Leuchtorgane von *Lampyris splendidula.*" ('Archiv für Mikr. Anatomie,' 1855.) See also Kölliker, 'Würzburg Phys. Med. Gesellschaft,' 1857.

somites. Each is a thin, whitish plate, one face of which is in contact with the transparent chitinous cuticula, while the other is in relation with the abdominal nerve-cord and the viscera. The sternal gives out much more light than the tergal face. The photogenic plate is distinguishable into two layers, one occupying its sternal and the other its tergal half. The former is yellowish and transparent, the latter white and opaque, in consequence of the multitude of strongly refracting granules which it contains. Tracheæ and nerves enter the tergal layer, and for the most part traverse it to terminate in the sternal layer, which alone is luminous. Each layer is composed of polygonal nucleated cells. The granules are doubly refractive, contain uric acid, and probably consist of urate of ammonia (Kölliker). Hence the cells of the layer which contain them are termed by Schulze the "urate cells," while he calls the others the "parenchyma cells." The branches of the tracheæ which ramify among the parenchyma cells end, like those of other parts of the body, in stellate nucleated corpuscles, one process of the corpuscle passing into a ramification of the trachea. Schulze is inclined to think that the other processes end in parenchyma cells.

The nerves of the photogenic plates are derived from the last abdominal ganglion; they branch out between the parenchyma cells into finer and finer branches, which eventually escape observation.

The female reproductive organs of insects consist of the ovarian tubes, or ovarioles, with their so-called peritoneal investments, and of the oviducts, which unite into a vagina; while a spermatheca, and, generally, accessory glands open into, or close to, the vagina.

The ovarioles may be few or very numerous. Each consists of an external structureless *membrana propria*, within which lies a solid columnar mass composed of cells. The anterior, usually tapering, end of this ovarian mass is composed of protoplasmic substance in which nuclei are imbedded, but in which the contours of the cells which they indicate are not distinguishable. Further back, some of

these nuclei enlarge, become surrounded by an accumulation of protoplasm, and constitute the primitive ova. Each primitive ovum is separated from its fellow by a layer of nucleated protoplasm which thus forms a capsule around it. In some insects, such as *Blatta*, the capsule is hardly distinguishable in those ova which lie between the smallest and those of middling size, which follow the former in order from before backwards. But, in the larger ova which succeed these, the cells of the ovicapsule rapidly enlarge in a direction perpendicular to the surface of the ovum, and constitute a very well-marked epithelial layer. I am inclined to believe that, for some time, an addition is made to the vitellus of the egg by these epithelial cells, and that they, in fact, play the part of vitelligenous cells. But however this may be, before long, a delicate structureless lamella appears on the surface of the vitellus and encloses the egg as a vitelline membrane. The epithelial cells of the ovicapsule next secrete from their surface a thicker, often ornamented, layer of chitinous substance, which constitutes the chorion, and the egg is complete.

The ovarian mass, therefore, as Waldeyer has justly pointed out, corresponds with one of the epithelial tubes of the ovary of a vertebrated animal, and the ovicapsules answer to Graafian follicles.

In some insects, as *Aphis*, the indifferent tissue of the anterior end of the ovarioles gives rise not only to ova and ovicapsular epithelium, but to large *vitelligenous cells.* These stay in the dilated anterior chamber of the ovarian tube. But each ovum is originally connected by continuity of substance with one of these cells, and the pedicle of connection may be traced even to the second and third ovum. It seems probable, therefore, that these "vitelligenous cells," for some time, supply material to the growing ova.

In most insects, similar vitelligenous cells are found; but they are situated at the anterior end of each ovicapsule, so that, as the column of ovicapsules lengthens by the addition of new ovicapsules to its anterior end, the vitelligenous cells are interposed between every two ova. The vitelline mem-

brane and the chorion first invest the posterior extremity and the sides of the ovum; and, for some time, leave an opening at the end of the ovum adjacent to the vitelligenous cells. This opening is usually only partially closed, and what remains of it constitutes the aperture or apertures, termed the *micropyle*, through which the spermatozoa enter when the egg is fecundated. The vitelligenous cells usually remain outside the ovum, and eventually undergo degeneration; but, in many *Diptera*, they become enclosed within the coats of the ovum and their substance is merged in that of the vitellus.

Dr. A. Brandt has proposed the term *panoistic* for ovaries of the first mode, and *meroistic* for those of the second and third modes of development of the ova here described. So far as is at present known, only the *Orthoptera* and the *Pulicidæ* possess panoistic ovaria.

The peritoneal coat of the ovarioles is a cellular structure, containing many tracheæ and, frequently, muscular fibres. It is usually extended beyond the anterior end of each ovariole into a filamentous process, which after uniting with those of the other ovarioles of the same side, is continued into the pericardial tissue. At its opposite extremity it passes into the walls of the oviduct, which are muscular and are lined by an epithelium.

The development of the ovaria has been traced in *Diptera* and *Lepidoptera*. Each ovary is, at first, a rounded mass of indifferent tissue, from which a filiform prolongation is given off backwards; this has not been traced into connection with any other organ, and appears to terminate by a free end. The mode of origin of this rudimentary, or primary, ovarium is unknown, but the first step towards the formation of the genital organs is the separation of the peripheral indifferent tissue from the central portion, and the division of the latter into as many elongated solid cellular bodies as ovarioles are to be formed. The peripheral cells become the peritoneal layer. Each cellular rudiment surrounds itself with a structureless membrane, and then elongates into an ovariole, some of the cells filling

the posterior end of which then become differentiated into the first primary ovum and its capsule, with or without vitelligenous cells. The contents of each ovariole must therefore be regarded as a column of generative cells, which instead of burrowing in the stroma of an ovary, and becoming divided into ovisacs, as in a vertebrated animal, grows straight backwards, and, as it grows, becomes divided into ovisacs, of which the oldest and most advanced is the hindermost.

Nothing is certainly known respecting the origin of the vagina or the oviducts, though it may be suspected that the posterior prolongations of the primary ovaries give rise to the latter.

The development of the testes takes place in the same manner as that of the ovaries, but the contents of the testicular tubes become converted into spermatozoa. The origin of the vasa deferentia is unknown.*

In most insects, the vitellus undergoes partial yelk-division. In some *Poduridæ*, however, complete division has been observed. The development of the blastoderm takes place in the same way as in other Arthropods, and the cephalic end of the embryo terminates in two procephalic lobes. In many insects, the periphery of the blastoderm, external to the longitudinal thickening which gives rise to the sternal region of the body, and which may be termed the

* The account given above of the structure of the ovarian tubes in *Blatta* and *Aphis*, is based on my own observations, which are in pretty close accordance with those of A. Brandt, "Ueber die Eiröhren der *Blatta* (*Periplaneta*) *orientalis*" ('Mém. de l'Acad. St. Pétersbourg,' tome xxi., 1874). The literature of the subject is somewhat extensive. See especially Leydig, "Die Eierstock und die Samentasche der Insecten" ('Nova Acta,' xxxiii., 1867); Lubbock, "The ova and pseudova of Insects" (Phil. Trans., 1858); Weismann, "Die nachembryonale Entwickelung der Musciden" ('Zeitschrift für Wiss. Zoologie,' xiv.); Bessels, "Entwickelung der Sexualdrüsen bei den Lepidopteren" ('Zeitschrift für Wiss. Zoologie,' 1857); and Von Siebold, 'Beiträge zur Parthenogenesis der Arthropoden,' 1871. The various forms of the micropyle and the structure of the chorion are dealt with by Leuckart, in his elaborate memoir, "Ueber die Micropyle und den feineren Bau der Schalenhaut bei den Insekteneiern" ('Müller's Archiv,' 1855.)

sternal band ('Keimstreif' of the German embryologists), gives off a lamina which grows inwards over the sternal face of the embryo, and eventually forms a complete investment thereto. The lamina may be formed by a single layer of cells, or it may, from the first, be a fold of the blastoderm and thus consist of two layers, the inner of which is continuous with the sternal band, and the outer with the blastoderm which invests the tergal surface of the vitellus. In the latter case, it becomes strictly comparable to the amnion of a vertebrated animal; and, when the folds have united in the middle line, the investment in question is distinguishable into an outer membrane, which answers to the *lamina serosa,* and an inner, which corresponds with the amnion proper of the vertebrate embryo. In some cases, the vitelline substance fills up the interval between the *lamina serosa* and the amnion, so that the sternal band and the latter form a sac plunged into the interior of the yelk.

The development of a more or less complete amniotic investment has been observed in *Orthoptera* (*Libellula*), *Coleoptera, Hemiptera, Hymenoptera, Lepidoptera,* and *Diptera,* but it does not appear to be universal.

Agamogenesis is of frequent occurrence among insects, and occurs under two extreme forms; in the one, the parent is a perfect female, while the germs have all the morphological characters of eggs, and to this the term *parthenogenesis* ought to be restricted.* In the other the parent has incomplete female genitalia, and the germs have not the ordinary characters of insect eggs.

In *Coccus* (*Lecanium*) *hesperidum,* in *Chermes abietis* and *pini,* no males have yet been observed; but the perfect females produce ova, out of which only females proceed. It is probable that many species of gall insects (*Cynips*) are in the same predicament.

* The excellent 'Beiträge zur Parthenogenesis' (1871) of Von Siebold is my chief authority for the statements in the text respecting Agamogenesis in Insects.

The unimpregnated, apterous, caterpillar-like females of the Lepidopterous genera *Psyche* and *Solenobia*, lay eggs out of which only females issue. The males occur but rarely and locally, and, from the impregnated eggs, males and females issue in about equal numbers.

Leuckart discovered that the ovaries of so-called neuters among wasps, hornets, humble-bees, and ants, often contain more or less well-developed eggs, and that in the wasps and humble-bees, such eggs are laid and develope young, the sex of which was not ascertained. Von Siebold has observed that the neuters of *Polistes gallica* are distinguished from the perfect fertilisable female, by little more than their smaller size, and that they possess completely developed female organs. These neuters, or rather, small females, laid eggs which developed, and gave rise only to male *Polistes*. The unimpregnated females of a Saw-fly, *Nematus ventricosus* (the larvæ of which are known as gooseberry caterpillars) regularly lay eggs, which develope and produce male offspring.

The terms *arrenotokous* and *thelytokous*, have been proposed by Leuckart and Von Siebold to denote those parthenogenetic females which produce male and female young respectively.

In the case of the Hive-bee, it has been ascertained that the queen either impregnates, or does not impregnate, the eggs when they are laid. The spermatheca, in which the spermatic fluid, introduced by the single act of copulation which takes place, is contained, contracts as the eggs pass along the vagina, in the former case, and remains passive in the latter. The unimpregnated eggs give rise to males or drones; the impregnated eggs to females, which become neuters with imperfect reproductive organs, or queens, with perfect organs, according to the nutriment which they receive.

In the *Aphides*, ova deposited by the impregnated females in the autumn are hatched in the spring, and give rise to forms which are very generally wingless, and bring forth living young. These may be either winged or wingless, and

are also viviparous. The number of successive viviparous broods thus produced, has no certain limit, but, so far as our present knowledge goes, is controlled only by temperature, and by the supply of food. *Aphides* kept in a warm room and well supplied with nourishment, have continued to propagate viviparously for four years.

On the setting in of cold weather, or, apparently, on the failure of nourishment alone, in some cases, males and females are produced by the viviparous forms. The males may possess wings, or may be devoid of them. The females appear invariably to be apterous. Copulation takes place and the eggs are laid.

Sometimes viviparous forms co-exist with the male or female forms, and some viviparous Aphides are known to hybernate.*

The viviparous forms differ essentially from the oviparous forms in the structure of their reproductive organs. They possess neither spermathecæ nor colleterial glands, both of which, as Von Siebold first demonstrated, are present in the females. The young are developed within organs which resemble the ovarioles of the true females in their disposition and may be termed *pseudovaries*. The terminal or anterior chamber of each pseudovarian tube is lined by an epithelium, which encloses a number of nucleated cells. One of the hindermost of these cells enlarges and becomes detached from the rest as a *pseudovum*. It then divides and gives rise to a cellular mass, distinguishable into a peripheral layer of clear cells and a central more granular substance, which becomes surrounded by a structureless cuticula. It is this cellular mass which gradually becomes fashioned into the body of a larval *Aphis*. A portion of the cells of which it is composed becomes con-

* Huxley, "On the Agamic Reproduction and Morphology of Aphis." ('Linnean Transactions,' 1857.)

The papers of M. Balbiani ('Ann. des Sciences Naturelles' 1869, 1870, and 1872) should be consulted, not only on account of their richness in details, but for the peculiar views which the author entertains respecting the nature of the reproductive process in the *Aphides*.

verted into a pseudovarium, and the development of new pseudova commences before the young leaves the body of its parent. It is obvious that this operation is comparable to a kind of budding. If the pseudovum remained adherent to the parental body, the analogy would be complete.*

The agamogenetic multiplication of *Cecidomyia*-larvæ is an essentially similar process. Professor Nicolas Wagner, of Kasan, † discovered that the larvæ of a Dipterous insect belonging to the genus *Cecidomyia*, or to a closely-allied form, (*Miastor*) multiply agamogenetically in the autumn, winter, and spring. In summer, the final terms of the successive broods of grubs thus produced are metamorphosed into males and females, which copulate and lay eggs. From these, larvæ which exhibit the same phenomena, emerge. In this case, the young are all developed from germs which are found lying loose in the perivisceral cavity of the parent, the body of which they destroy and burst in order to become free. Leuckart, Metschnikoff, and Ganin,‡ have shown that these germs are detached from the pseudovarium, which occupies the place of the rudimentary ovarium ordinarily found in larvæ; and that each represents the egg-chamber of an ordinary insect ovariole with its epithelial capsule, ovum and vitelligenous cells.

In the ordinary process of growth of an insect, from the time it leaves the egg until it attains the adult condition, every marked change in the outward form of the

* Leydig ("Die Eierstock und die Samentasche der Insecten," 'Nova Acta,' 1867) affirms that in November he has met with *Aphides* in which, in the same animal, some of the ovarian tubes contain fully formed ova, and others pseud-ova, undergoing their ordinary method of development. Unfortunately no information is afforded as to whether these aphides possessed a spermatheca, and showed evidence of impregnation or not. The occurrence of agamogenesis alongside of sexual propagation is in itself nothing unprecedented, *e.g. Pyrosoma*.

† K. E. von Baer, "Bericht." ('Bulletin Acad. St. Pétersbourg,' 1863.)

‡ Leuckart, "Die ungeschlechtliche Vermehrung der Cecidomyienlarven" ('Göttinger Nachrichten,' 1865); K. von Baer, "Ueber Prof. Nic. Wagner's Entdeckung," &c. ('Mélanges biologiques tirés du Bulletin de l'Acad Imp. des Sciences de St. Pétersbourg,' 1865).

body, or of its appendages, is accompanied by a shedding of the cuticula. In some cases the modification effected at each ecdysis is very slight, and the moultings of the cuticle are numerous, amounting in a species of Day-fly (*Chloeon*), described by Sir John Lubbock, to as many as twenty. In such a case as this, the structure of the adult is gradually substituted for that of the larva, and the organs of the larva, for the most part, pass into those of the adult.

The like holds good of some insects which undergo metamorphosis, that is to say, in which a quiescent pupal condition is interposed between the active larval and the active imaginal states. Herold and Newport have described at length the series of changes by which the elongated ganglionic chain of the Lepidopterous caterpillar is converted into the much more highly concentrated nervous system of the Butterfly; and Weismann has shown by what gradual steps the apodal *Corethra*-larva acquires the character of the Dipterous imago. But, in the Flesh-flies (*Musca*), and probably in many other members of the division of the *Diptera* to which they belong, the apodal maggot, when it leaves the egg, carries in the interior of its body certain regularly arranged discoidal masses of indifferent tissue, which are termed *imaginal disks.** Of these, twelve are situated in the thoracic region, two on each side of each thoracic segment, while two others lie in front of the pro-thoracic disks. These imaginal disks undergo little or no change until the larva encloses itself in its hardened last-shed cuticle, and becomes a pupa. But they then rapidly enlarge; each of the sternal thoracic disks gives rise to a leg and to its half of the sternal region of the thorax, while the tergal disks develope into the tergal halves of the corresponding somites, with their appendages, the wings and the halteres. The anterior pair of disks originate the head and proboscis of the fly. As the imaginal disks develope, the pre-existing organs contained

* See the remarkable memoir of Weismann, 'Die nachembryonale Entwickelung der Musciden.'

in the head and thorax of the larva, undergo complete or partial resolution. On the other hand, the abdomen of the fly is produced by the continuous modification of the constituents of the larval abdomen.

As in the *Crustacea*, so in *Insecta*, the parasitic habit is

Fig. 111.

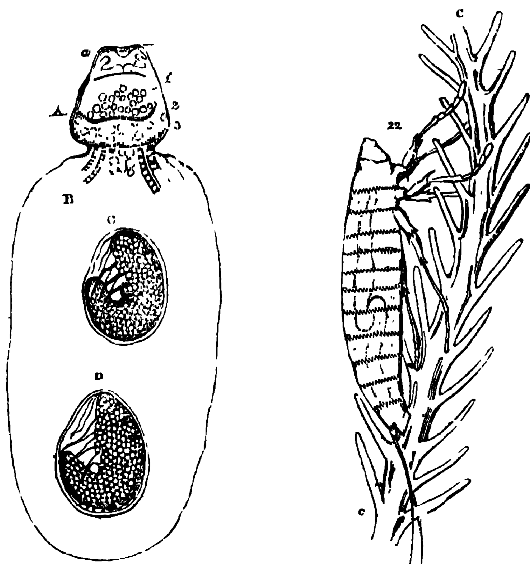


Fig. 111.—The left-hand figure represents an adult female of *Stylops aterrimus* containing two nearly hatched eggs, and the right-hand figure, a newly born larva of *Stylops* on a hair of *Andræna Trimmerana*. A, ventral surface of the thorax; B, the abdomen; *a*, mandibles; *b*, labial plates and mouth; *c*, vulva; 1, 2, 3, the three thoracic segments united. (After Newport.)

accompanied by extreme modification of form. In this respect the *Strepsiptera*, which are parasitic upon Bees, present a remarkable history. The female (Fig. 111) has the form of a sac with a short neck, and never leaves the body of the Hymenopteran in which she is parasitic. The males,

on the contrary, are exceedingly active insects provided with a single pair of wings, which are attached to the metathorax, while the mesothorax has a pair of twisted appendages in the place of wings.

The larvæ of both males and females when they leave the egg, are minute active hexapod insects (Fig. 111), with rudimentary manducatory organs, and are found creeping about between and on the hairs with which the abdomen of their host is provided. In this condition they are carried into the nests of the bees, and they attack the larvæ of the latter, boring their way through the integument into the abdominal cavity of the grub. Here they cast their cuticle and become changed into sluggish apodal grubs, provided with a mouth, with rudimentary jaws, and with an alimentary sac, but devoid of an anus. About the time that the Hymenopterous larva passes into its imago state, the Strepsipteral larva thrusts the anterior end of its body (the so-called cephalo-thorax) between two of the abdominal segments of the bee, so that it projects externally. The male becomes a pupa, and eventually makes its way out as a winged insect The female on the other hand undergoes little change of outward form, but presents an opening, which plays the part of a vulva, and enables the male to effect the fecundation of the eggs. These are developed within the body of the female, and make their way out by the cleft in question.*

The Ichneumon-flies deposit their eggs within the bodies of the larvæ of other insects, and the grubs thence hatched devour the corpus adiposum of their host. The larvæ of some of these parasites (*Platygaster*, *Teleas*), described by Ganin † are extraordinarily unlike other insect larvæ, and have a certain resemblance to *Copepoda*.

* See Von Siebold, "Ueber Strepsipteren" ('Archiv für Naturgeschichte,' 1843), and Newport, "Natural History &c. of the Oil-beetle, *Meloe*" (Linn. Trans. 1847).

† 'Zeitschr. für Zoologie,' 1869.

CHAPTER VIII.

THE POLYZOA, THE BRACHIOPODA, AND THE MOLLUSCA.

HOWEVER diverse in outward appearance and in complexity of organisation the multitudinous forms of animals which have been described in the preceding four chapters (Chap. IV. to VII.) may be, the student passes from one to the other, by easy and natural gradations, from the simple Turbellarian at the bottom, to the most highly differentiated Arthropod at the summit of the series. But with the higher *Crustacea*, *Arachnida* and *Insecta* the scale ends; from none of these are we led to any higher form of animal life.

The Cuttle-fish, the Whelk, the Snail, and the other innumerable forms of animals with univalve, bivalve, and multivalve shells, which are commonly known as *Mollusca*, are so widely different, not only from the *Arthropoda*, but from all the higher members of the group of Worms (Chap. V.) that any connection with these seems, at first, to be wanting. The segmentation of the body, which is so conspicuous a feature of the greater number of the members of the series which ends with the Arthropods, is absent; limbs are wanting; instead of the equality of the neural and hæmal faces of the bilaterally symmetrical body, and the consequent remoteness of the oral and anal apertures, which is usual among the Arthropods and Worms, these two faces are usually unequal. The hæmal face is often produced into a longer or shorter cone; the anus is, as a rule, approximated to the mouth; and, very often, the hæmal face of the body is asymmetrical.

The higher Mollusks, in fact, form the final term of a

series of their own, which commences in the *Polyzoa*, with animals which have many resemblances to the *Rotifera*.

The POLYZOA or BRYOZOA.—In outward form these animals bear a general likeness to the Sertularian *Hydrozoa*, with which they were formerly confounded under the name of "Corallines." Like the Sertularians, they almost always form compound aggregations, produced by repeated acts of gemmation from the primitively single embryo, and have a hard cuticular exoskeleton, which remains when the soft parts decay. The compound organism thus formed is

Fig. 112.

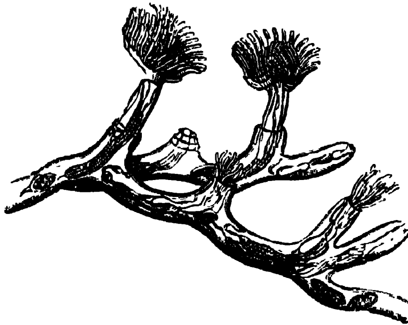


Fig. 112.—A portion of the polyzoarium of *Plumatella repens* (after Allman).*

termed a *Polyzoarium* (Fig. 112), and each zooid which buds from the common stock is a *Polypide*. The outer, chitinous or calcified, cuticular exoskeleton, is termed the *ectocyst*, and, as the rest of the body of the polypide is contained in, or can be retracted into, the hard case thus formed, it is commonly termed a "cell."

The proper ectoderm, with the parietal layer of the mesoderm which lines and secretes this cell, is termed the *endocyst*. The mouth is situated on a disk, termed the

* 'Monograph of the Fresh-water Polyzoa,' 1856.

lophophore, at the free end of the polypide; and the margins of the *lophophore* are produced into a number of richly ciliated *tentacula.* At the oral aperture, the ectoderm passes into the endodermal lining of the ali-

Fig. 113.

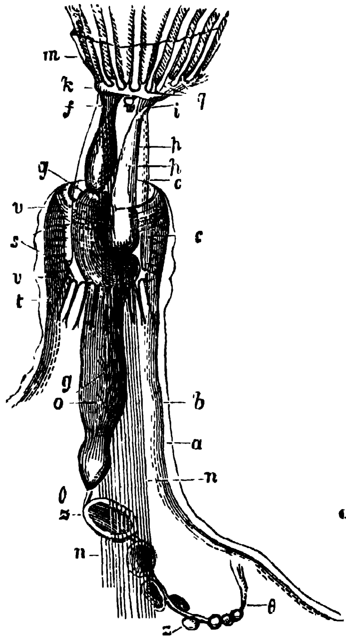


Fig. 113.—*Plumatella repens.*—A single cell more magnified; *a*, ectocyst; *b*, endocyst; *m*, calyx at the base of the ciliated tentacula borne by the disk or lophophore; *k*, mouth; *f*, gullet; *g g*, stomach; *h*, intestine; *i*, anus; *n*, muscles; *w*, nervous ganglion; *z*, statoblasts; *θ*, funiculus. (After Allman.)

mentary canal, which is almost always divided into three portions, a long and wide pharynx, a spacious stomach, and a narrow intestine. The latter is always bent up nearly

parallel with the pharynx, and terminates in an anus situated beside the mouth. As the nervous ganglion is placed between the mouth and the anus, the flexure of the intestine is *neural*,* and the hæmal face of the body is developed greatly in excess of the neural face. A wide perivisceral cavity occupies the interval between the alimentary canal and the parietes of the body, and sometimes the walls of this cavity are ciliated. Very generally, the gastric division of the alimentary canal is connected with the parietes of the body by a sort of ligament, the *funiculus*, or *gastro-parietal band*. Circular and longitudinal muscular fibres, which frequently exhibit distinct transverse striations, may be developed in the body-wall; and there are usually special muscles for the retraction of the lophophore within the cell, and others for the closing and opening of the opercular apparatus, with which many species are provided.

The single nervous ganglion is situated, as has been stated, between the oral and the anal apertures. In *Serialaria, Scrupocellaria* and some other genera, nervous cords and plexuses connecting the ganglia of the several polypides and constituting what F. Müller† terms a "colonial nervous system," have been described. But it is not yet certain that these cords and plexuses are really nerves. It is doubtful if there are any special organs of sense, unless a lobed process—the *epistoma*,—which overhangs the mouth in many fresh-water Polyzoa, be of this nature. The ectoderm of that region of the body which lies immediately beneath the tentacula is always soft and flexible; and when the lophophore is retracted, becomes invaginated, so as to form a sheath, by which the tentacles are protected. Sometimes, as in the *Ctenostomata*,‡ this sheath

* In dealing with the morphological relations of the parts of Mollusks, it is very necessary to employ a terminology which shall be independent of the ordinary position of the animals. I therefore term that face of the body on which the chief nervous centres, or the pedal ganglia (when such are separately distinguishable) are placed, *neural*, and the opposite *hæmal*.

† 'Archiv für Anatomie,' 1860.

‡ Farre, "Observations on the minute structure of some of the

is surrounded by a circle of chitinous filaments, which, when the tentacles are retracted, furnish a protective outer covering to them. And, sometimes, as in the *Cheilostomata*,* part of the ectocyst of the polype cell is disposed in such a manner as to constitute a moveable lid, which shuts down on the retracted polypide. This *operculum* is placed on the opposite side of the polypide to that on which the nervous ganglion is situated.

In many genera, the cells are provided with flagelliform

Fig. 114.

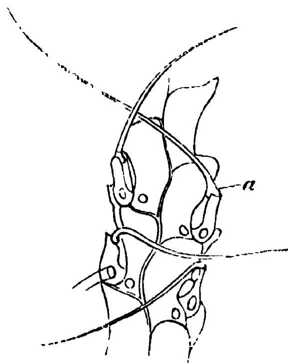


Fig. 114.—*Scrupocillaria ferox.*—A small portion of a polyzoarium, showing the vibracula (*a*). (After Busk.)†

appendages—the *vibracula* (Fig. 114). These are usually articulated with short dilated processes of the ectocyst, and

higher forms of Polypi" ('Phil. Trans.' 1837). Reichert, "Ueber *Zoobotryon pellucidus*" ('Abh. d. Königl. Akad. der Wissenschaften,' Berlin, 186·).

* Busk, 'Catalogue of the Marine Polyzoa in the British Museum: Chilostomata,' 1852-54, See for this group Nitsche's recent important "Beiträge zur Kenntniss der Bryozoen" ('Zeitschrift für Wiss. Zoologie,' 1869-71).

† 'Catalogue of Marine Polyzoa,' 18.)2.

execute constant lashing movements. In others, bodies shaped like birds' heads, with a movable mandible, and either seated upon slender and flexible peduncles or sessile, snap incessantly. Sometimes these last, which are termed *avicularia* (Fig. 115), are present along with vibracula.

Fig 115.

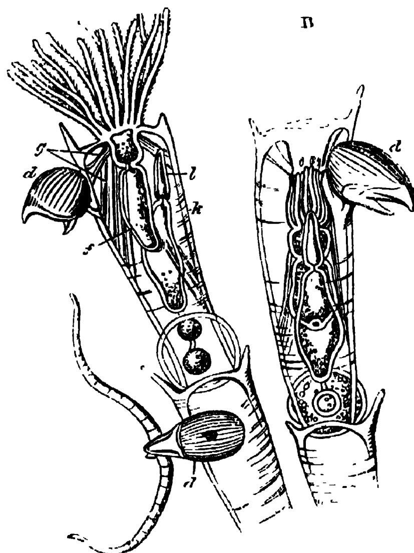


Fig. 115.—*Bugula avicularia.*—A, part of the polyzoarium viewed from the neural side, showing the tentacles of a polypide protruded from its cell (*k*); the intestine (*l*) and the stomach and gullet (*f*); *g*, retractor muscles; *d*, *d*, avicularia. One of these is holding a minute worm which it has seized. In front of this is seen an ovicell.
B, a retracted polypide with an avicularium (*d*), viewed from the hæmal or dorsal side.

The dilated bases of the vibracula contain muscles by the contraction of which the flagelliform appendage is moved. In the avicularia, a large adductor muscle, which takes its origin from the greater part of the inner surface

of the "head," is attached by a slender tendon to the "mandible" on the one side of the hinge line, while a smaller divaricator muscle is fixed to the other side. The mechanism of adduction and divarication of the mandible is quite similar to that by which the dorsal valve of the shell of an articulated Brachiopod is moved upon the ventral valve.

Male and female reproductive organs are usually combined in the same polypide. They are cellular masses, developed in the funiculus, or in the parietes of the body, whence the ova or spermatozoa are detached into the perivisceral cavity. They sometimes pass thence, and undergo the first stages of their development in dilatations of the wall of the body, termed *ovicells.*

Multiplication by gemmation occurs throughout the group, but the buds usually remain adherent to the stock. In *Loxosoma* and *Pedicellina,* however, the buds become detached.

Some *Polyzoa* multiply agamogenetically by a kind of gemmule developed in the *funiculus,* provided with a peculiar shell, and termed a *statoblast.*

With these general characters, the *Polyzoa* present an interesting series of modifications. They have been divided by Nitsche into two groups—the *Entoprocta,* in which the anus lies within the circle of tentacles; and the *Ectoprocta,* in which it lies outside this circle. In the former division, the genus *Loxosoma,** which attaches itself to Sertularians and to other *Polyzoa,* is particularly noteworthy. It is a small stalked animal, and the superior wider end of the body is an obliquely truncated disk, the margins of which are elongated into ten ciliated processes. The mouth is a transversely elongated, slit-like aperture on the lower side of the tentacular circlet. A long œsophagus connects this with a globular cæcal gastric sac. From the midst of the

* Kowalewsky, "Beiträge zur Anatomie und Entwickelungsgeschichte des Loxosoma neapolitanum" ('Mém. de l'Acad. de St. Pétersbourg,' 1866). Oscar Schmidt, "Die Gattung Loxosoma" ('Archiv für Mikr. Anat.' 1875).

disk, a conical prominence, the summit of which bears the anus, is situated. The sexes are united, the ovaries and testes being situated on each side of the stomach, and the spermatozoa pass directly into the ovaries. No nervous system has yet been made out in *Loxosoma*. The animal is fixed by the truncated extremity of its narrow stalk-like end; and this stalk contains a gland, the duct of which opens in the centre of the face of attachment.

Loxosoma appears to multiply by budding, but the apparent buds are really one of two kinds of embryos developed from the impregnated ova. The other kind of embryo becomes a gastrula, with a large post-oral ciliated disk, like a mesotrochal annelid larva, and its ultimate fate has not yet been traced.

The *Ectoprocta* are divided into the *Gymnolæmata*, which have a circular lophophore, and no epistoma; and the *Phylactolæmata*,* which possess an epistoma, and usually have the lophophore prolonged into two lobes, so as to be horse-shoe-shaped; whence the term *hippocrepian* applied to such *Polyzoa*.

Among the *Gymnolæmata* are distinguished; the *Cyclostomata*, in which the opening of the cell is round and has no opercular structures; the *Ctenostomata* (*suprà*), and the *Cheilostomata* (*suprà*).

All the *Phylactolæmata* are inhabitants of fresh water; while all the *Gymnolæmata*, except *Paludicella*, are marine.

The polyzoarium of *Cristatella* is free and creeps about as a whole; and that of *Lunulites* is free, at any rate in the adult condition.

In the fresh-water *Polyzoa*, the impregnated ovum gives rise to a saccular planuliform embryo, which is covered externally with cilia. From one end of this *cystid*, one or more polypides are developed from thickenings of the wall of the sac.

* See Dumortier and Van Beneden, "Histoire Naturelle d. Polypes composées d'eau douce" ('Mém. de l'Acad. Royale de Bruxelles,' 1850); the monograph of Allman cited above; and Nitsche's "Beitrage."

In the Gymnolæmatous genera *Bugula*, *Scrupocellaria*, and *Bicellaria*, the embryo is ciliated, and provided with a mouth and with eye-spots. After swimming about for some time, it loses its cilia, fixes itself, acquires a chitinous outer coat, and becomes a mere sac or, cystid, in which a polypide is developed by gemmation, and gives rise to the first cell of the polyzoarium.

Schneider* has shown that the anomalous *Cyphonautes*, which he considers to resemble *Actinotrocha*, and which is enclosed in a bivalve shell, is the larva of *Membranipora pilosa*. It is provided with an intestine, and with largely developed ciliated motor bands. But when it attaches itself, all these organs disappear, and the larva passes into the condition of a cystid, from which a polypide is developed, as in the foregoing cases.

Hence, it has been pointed out that the characteristic polypide of the ectoproctous *Polyzoa* is a structure developed from the cystid, in much the same way as the *Tænia*-head is developed from its saccular embryo; or as the *Cercaria* is developed from the sporocyst or *Redia*; the cystid of the *Phylactolæmata* being comparable to a sporocyst, and that of *Membranipora* to a *Redia*. But, without altogether denying the justice of this comparison, it may be suggested that the cystid is comparable to a vesicular morula, and that the mode of development of the alimentary canal of the polypide corresponds with that of the formation of an alimentary sac by invagination. If this view of the case be correct, the perivisceral cavity in the *Polyzoa* is a blastocœle, more or less modified by the development of the mesoderm.

The only known representative of the genus *Rhabdopleura*† is an aberrant Polyzoon which presents many interesting peculiarities. The polyzoarium consists of a creeping stem from which erect branches, each of which

* "Zur Entwickelungsgeschichte und systematischen Stellung der Bryozoen und Gephyreen." ('Archiv für Mikr. Anat.' 1869.)

† See the papers of Allman and G. O. Sars, 'Quarterly Journal of Microscopical Science,' 1869 and 1874.

ends in a circular aperture and constitutes the cell of a polypide, arise. The cavity of the stem is divided by transverse septa, and its centre is traversed by a hollow chitinous cord, which passes through and is attached to the septa.

The lophophore resembles that of the hippocrepian *Phylactolæmata* in being produced into two arms, fringed with a double series of tentacula. These arms are longer, narrower, and more cylindrical than in any other *Polyzoa*, and, thus far, approach the arms of the *Brachiopoda*. Furthermore the tentacula are confined to the arms, which are very flexible. Between the bases of the arms there is a rounded or pentagonal disk with raised and ciliated edges, which occupies the place of the epistoma in the phylactolæmatous *Polyzoa*. The mouth is situated beneath the free margin of this disk, on the opposite side to the anus, and to that towards which the arms are turned. The animal is attached to the bottom of its cell, or rather to the endosarc of the stem, by means of a long contractile pedicle, by which its retraction is effected. According to Sars, it protrudes itself by climbing up the wall of its tubular cell by means of the disk. Professor Lankester's comparison of the polypide of *Rhabdopleura* to the embryo *Pisidium*,* appears to me to be fully justified. The branchiæ of *Nucula*, in form and position, present no little resemblance to the arms of *Rhabdopleura*, though these, like the arms of the *Brachiopoda*, are probably more strictly comparable to the labial palpi of the Lamellibranchs.

Polyzoa occur in the fossil state from the Silurian epoch to the present day, and the oldest forms are referable to the groups which now exist.

The Brachiopoda.—The *Brachiopoda* are all marine animals provided with a bivalve shell, and are usually fixed by a peduncle which passes between the two valves in the

* "On the developmental history of the Mollusca." ('Phil. Trans.' 1874.)

centre of the hinge line, or the region which answers to it, in those Brachiopods which have no proper hinge. They never multiply by gemmation, nor give rise to compound organisms. The shell is always inequivalve and equilateral; that is to say, each valve is symmetrical within itself and more or less unlike the other valve. The shell is a cuticular structure secreted by the ectoderm, and consists of a membranous basis, hardened by the deposit of calcareous salts, sometimes containing a large proportion of phosphate of lime (*Lingula*).

In many Brachiopods, variously formed calcareous spicula, or minute plates, are found in the walls of the perivisceral cavity, and of the greater sinuses; and also in the arms and cirri, and sometimes these unite together so as to form an almost continuous skeleton.*

The body, or rather that part of it which contains the chief viscera, is often small relatively to the valves of the shell, and the integument is produced into two broad lobes, which line so much of the interior of the valves as the visceral mass oes not occupy. The free edges of these lobes are thickened, and are beset with numerous fine chitinous setæ like those found in Annelids, and like them lodged in sacs. Between the two lobes of the mantle, or *pallium*, is the pallial chamber, bounded behind by the anterior wall of the visceral mass. In the middle line, this wall presents the oral aperture, which is seated in the midst of a wider or narrower area, the margins of which are provided with numerous ciliated tentacula.

In *Argiope*, the oral area occupies a large part of that lobe of the mantle which is ordinarily termed dorsal, and its margins are simply indented by three deep sinuations. In *Thecidium*, the sinuations are deeper, and the folds of the oral area thus produced, narrower. But in most Brachiopods the oral area is narrowed to a mere groove, and is produced on each side of the mouth into a long spirally-

* These have been described by Woodward, Lacaze-Duthiers and especially by Eudes Deslongchamps, 'Recherches sur l'organisation du Manteau chez les Brachiopodes articulés,' 1864.

coiled arm, fringed with tentacles; whence the name of *Brachiopoda*, applied to the group.

In this case, the tentacula disappear from the anterior margin of the oral disk in the region of the mouth, and are replaced by a lip-like ridge. Each arm contains a canal, which ends in a sac at the side of the mouth.

In *Waldheimia* (Fig. 116), the two arms are united together and their distal portions coiled into a horizontal spiral. In many genera, the margins of the oral area or arms are fixed to processes of the dorsal valve of the shell.* In this case the arms are not protrusible; but, according to the observations of Morse,† they can be straightened and extended beyond the shell in *Rhynchonella*, which has no brachial skeleton,.

The alimentary canal consists of an œsophagus, a stomach, provided with hepatic follicles, and an intestine. In the majority of existing genera the latter is short, and ends in a cæcum in the middle line of the body (*e.g. Waldheimia*); in others it is long, and opens into the pallial chamber on the right side of the mouth (*e.g. Lingula*, *Discina* and *Crania*).

The alimentary canal is invested by an outer coat—the so-called peritoneum,—by which it is suspended, as by a mesentery, in a spacious "perivisceral" cavity. The walls of this cavity are provided with cilia, the working of which keeps up a circulation of the contained fluid. Lateral processes of this coat—the *gastro-parietal* and *ileo-parietal bands*—connect the gastric and intestinal divisions of the alimentary canal respectively, with the parietes.‡

From the perivisceral cavity, sinus-like, branched prolongations extend into each lobe of the mantle, and end cæcally at its margins. The lobes of the mantle are pro-

* See, for excellent figures of these arrangements, and for the shells and external form of the body in general, Woodward's 'Manual of the Mollusca.'

† "On the systematic position of the Brachiopoda." (Proceedings of the Boston Society of Natural History, 1873.)

‡ Huxley, "Contributions to the Anatomy of the Brachiopoda" (Proceedings of the Royal Society, 1854); and Hancock, "On the organisation of the Brachiopoda" ('Phil. Trans.' 1858).

Fig. 116.

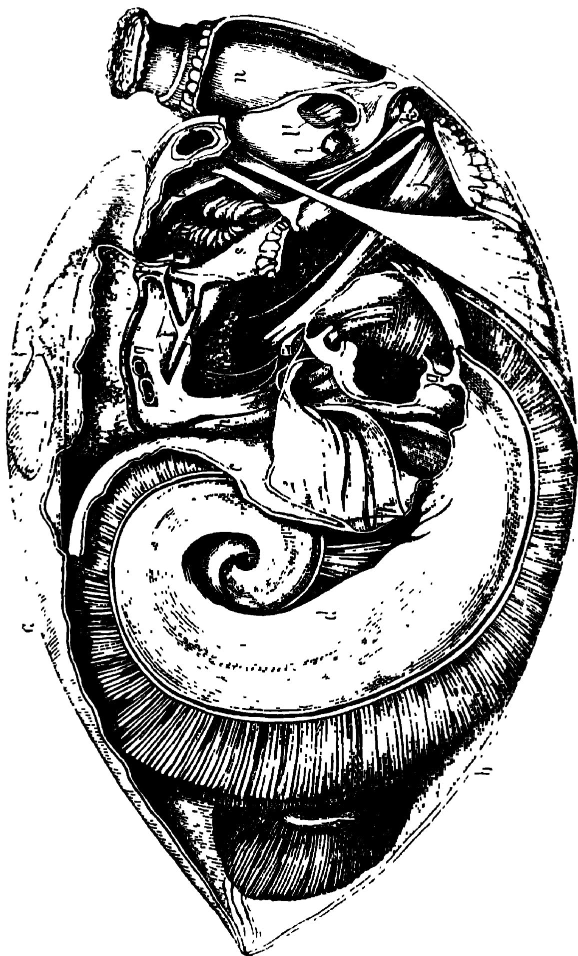


Fig. 116.—Lateral view of the viscera of *Waldheimia australis* (after Hancock, "On the Organization of the Brachiopoda," Phil. Trans. 1858).—*a*, 'dorsal' layer of mantle; *b*, 'ventral' layer; *c*, anterior

walls of the body between the mantle lobes; *d*, arms; *p*, gullet; *q*, stomach with cut biliary ducts of the left side. *r*, right hepatic mass; *s*, intestine ending cæcally below; *v*, so-called "auricles"; *o*, the right "pseudo-heart," the left being almost wholly removed; *w*, pyriform vesicle fixed at the back of the stomach; *z*, œsophageal ganglia; *i*, *j*, adductor; *k*, divaricator; *l*, adjustor muscles; *n*, peduncles.

bably, together with the ciliated tentacula, the seat of the respiratory function. The sinuses of the pallial lobes of *Lingula* give rise to numerous highly contractile, teat-like, processes, or *ampullæ*. During life the circulating fluid can be seen rapidly coursing into and out of each ampulla in turn (Morse, *l.c.* p. 33).

The perivisceral cavity communicates with the pallial chamber by at fewest two, and sometimes four (*Rhynchonella*) tubular organs, which have been described as hearts,* but are now known to have no such nature.

Each of these organs is shaped like a funnel, the wide portion which opens into the perivisceral cavity, being much plaited and folded, and separated by a constriction from the narrower part, which answers to the pipe of the funnel. The latter, passing obliquely through the anterior wall of the visceral chamber, ends by a small aperture in the pallial cavity. Prof. Morse has observed the passage of the eggs through these organs in *Terebratulina septentrionalis*. They are drawn into the open end of the funnel by the action of the cilia with which its surface is covered, and enter the pallial cavity by the aperture just mentioned. It is probable that these "pseudo-hearts" subserve the function both of renal organs and of genital ducts; and that they are the homologues of the organs of Bojanus of other mollusks, and of the segmental organs of worms.

Between the ectoderm and the lining membrane of the prolongations of the perivisceral cavity in the mantle; and between the endoderm, the ectoderm, and the lining membrane of the perivisceral cavity itself, there is an inter-

* Owen, "Lettre sur l'appareil de la circulation chez les Mollusques de la classe des Brachiopodes." ('Annales des Sciences Naturelles,' 1845.)

space, broken up into many anastomosing canals, which I conceive to represent a large part of the proper blood system.

Vesicular dilatations of the walls of these canals found at the back of the stomach, and in some other localities, in the Brachiopods with articulate shells, have been regarded as hearts, but observations on the living animals, made by various investigators, show that they are not contractile and their function is unknown. Although the existence of a direct communication between the perivisceral chamber and the blood canals has not been demonstrated, it is very probable that the perivisceral chamber really forms part of the blood-vascular system.

Muscles for the adduction and divarication of the valves of the shell, and for effecting the other movements of the animals, are well developed in the *Brachiopoda.** They are to a great extent striated.

The nervous system of the articulated Brachiopods, in which it has been best made out, consists of a relatively thick ganglionic band on the ventral side of the mouth, the ends of which are united by a commissural cord, which surrounds the gullet, and bears two small ganglionic enlargements. The latter probably answer to the cerebral, the former to the pedal, ganglia of the *Lamellibranchiata.* Immediately behind the pedal mass, from which two large nerves to the dorsal or anterior lobe of the mantle are given off, are two elongated ganglia, connected by a commissure of their own, which possibly correspond with the parieto-splanchnic ganglia of the higher Mollusks. The nerves to the ventral lobe of the mantle and those to the peduncle arise from these ganglia.

In the inarticulated Brachiopods, our knowledge of the nervous system is very imperfect. In *Lingula,* Professor Owen has described two lateral nerve cords, and the observation has been confirmed by Gratiolet and Morse. The

* See Hancock (l. c.). Owen, Introduction to Davidson's 'Fossil Brachiopoda' (Memoirs of the Palæontographical Society, and Transactions of the Zoological Society of London, 1835).

latter anatomist finds similar cords in *Discina*, and Gratiolet has described an œsophageal ring in *Lingula.**

The reproductive organs are lodged in the perivisceral cavity or its prolongations, and are apparently always contained in processes of the lining membrane of that cavity. It is not clear whether hermaphrodism is the rule or the exception. *Thecidium*, however, has been shown by Lacaze-Duthiers to be diœcious; and, according to Morse, the sexes are distinct in *Terebratulina* and *Discina*.

The development of the *Brachiopoda*, notwithstanding the important observations of F. Muller,† Lacaze-Duthiers,‡ and especially of Morse,§ stood much in need of further elucidation (especially in regard to the earlier conditions of the embryo), until quite recently, when the investigations of Kowalewsky || filled up the hiatus in our knowledge for the genera *Argiope*, *Thecidium*, *Terebratula*, and *Terebratulina*. The egg becomes converted into a vesicular morula, in which an alimentary sac is developed by invagination, and this sac gives off, as in *Sagitta*, two diverticula, which become shut off from the alimentary canal, and are converted into the perivisceral cavity. The latter, therefore, is an enterocœle. The embryo elongates, and constrictions divide it into three segments, of which the anterior becomes fringed with long cilia, and developes eye-spots. Thus the young Brachiopod acquires a great resemblance to an ordinary Annelid larva. The resemblance is increased by the appearance of four bundles of setæ on the middle segment, which becomes produced into a sort of hood, the free edges of which are at first turned backwards and bear

* "Recherches pour servir à l'histoire des Brachiopodes." ('Journal de Conchyliologie, 1860.)

† "Beschreibung einer Brachiopoden-larva." ('Archiv für Anat.,' 1860.)

‡ "Histoire de la Thécidée." ('Ann. d'Hist. Nat.,' 1861.)

§ "On the early stages of *Terebrutulina septentrionalis*" ('Memoirs of the Boston Society of Natural History,' 1869), and the memoir already cited.

|| Contained in a memoir, published at Moscow in 1874, for which I am indebted to the courtesy of the author. It is in Russian; but I have been able to acquaint myself with its contents, to some extent, by the aid of a friend.

these setæ. As the larva grows, the third segment becomes truncated at the end, and furnishes a surface (provided with a shell gland? *infrà*), by which the larva attaches itself. At the same time, the first, or præstomial segment, atrophies, and the setigerous hood developed from the middle segment is retroverted, rapidly grows, and gives rise to the lobes of the mantle, on which the valves of the shell are developed.

The resemblance of the larval Brachiopod to a Polyzoon, and especially to *Loxosoma*, is striking, and fully bears out the conclusion as to the affinity of the *Polyzoa* with the *Brachiopoda* which results from the study of their adult structure. On the other hand, the development of the *Brachiopoda* no less strongly testifies to their close relations with the Worms.*

In the course of the previous pages the terms dorsal and ventral have been employed in the sense in which they are conventionally used by conchologists. But an interesting question, and one not easy to settle is, what relation do these dorsal and ventral regions of a Brachiopod bear to the neural and hæmal regions of a Polyzoon, or to those of a Lamellibranch, or of a Gasteropod?

If we compare one of the articulated Brachiopods, such as *Waldheimia*, in its shell, with a polypide of a Cheilostomatous Polyzoon in its cell, the dorsal valve will appear to answer to the operculum, and the ventral valve to the cell. If this comparison be just, the two lobes of the mantle of the Brachiopod must both belong to the dorsal or hæmal aspect of the body; that which corresponds with the so-called dorsal valve of the shell being the anterior, and that which lines the ventral valve of the shell being the posterior lobe. And the region of the anterior wall of the pallial cavity

* The acceptance of the view originally propounded by Steenstrup and so ably urged by Professor Morse, respecting the affinities of the Brachiopods with the Worms (Proceedings of Boston Society of Natural History, 1873), does not to my mind weaken the opinion I have always held as to their affinities with the *Polyzoa*, on the one hand, and with the higher *Mollusca*, on the other.

which lies behind or below the mouth, will answer to the neural aspect of the Polyzoon.

On the other hand, if the segments of the body of the larval Brachiopod are true somites, and the discoidal surface of the hindermost corresponds with the similarly formed end of the larva of *Lacinularia*, as Professor Morse suggests, the dorsal lobe of the mantle will, as before, represent part of the hæmal surface of the body, but the ventral lobe will belong to its neural surface—and can no longer properly be termed mantle, but will rather answer to the foot of one of the higher Mollusca.

The *Brachiopoda* are distinguishable into two groups, the *Articulata* and the *Inarticulata*. In the *Articulata*, the two valves are united by a hinge, and the ventral valve is usually provided with teeth, which are received in sockets of the dorsal valve. The gullet ascends in the middle line towards the dorsal valve, and the intestine descends towards the opposite, or ventral, valve, and there ends in a cæcum. The dorsal valve often gives rise to spiral or looped shelly processes to which the arms are attached. The valves are brought together by a pair of adductor muscles, which pass directly from valve to valve; and they are separated by divaricator muscles, which run obliquely from the ventral valve to a median process (the *cardinal process*) of the hinge-line of the dorsal valve. The impressions of the attachments of these muscles on the inner surfaces of the valves have considerable systematic importance. Very often the ventral valve is produced into a sort of spout, through which passes the peduncle by which the animal is attached to rocks. At the sides of the visceral chamber the thickened edge of the dorsal lobe of the mantle passes into that of the ventral lobe.

The substance of the shell is very often traversed by numerous canals perpendicular to its surface, which contain prolongations of the mantle.*

* The structure of the shell has been particularly studied by Carpenter. ('Reports of the British Association,' 1844–1847, and Introduction to Davidson's 'Fossil Brachiopoda.') See also King,

This division contains the families of—(1) The *Terebratulidæ*, (2) the *Spiriferidæ*, (3) the *Rhynchonellidæ*, (4) the *Orthidæ*, and (5) the *Productidæ*, of which the second, fourth, and fifth are extinct and almost wholly palæozoic, no species extending beyond the lias, while the majority of the species of the other two families are also extinct.

The family of the *Terebratulidæ*, which is not certainly known to occur in formations older than the Devonian, is the only one in which, since the end of the palæozoic epoch, numerous new generic types appear.*

The *Inarticulata* have no hinge; the intestine opens into the cavity of the mantle, the margins of the lobes of which are completely separate. Some have a long peduncle (*Lingula*), others are fixed by a plug which passes through an aperture or notch of one valve (*Discina*), or by the surface of one valve (*Crania*). There is no brachial skeleton, and the arrangement of the muscles is in many respects different from that which obtains in the articulated division.

Species of all these families, except the *Spiriferidæ*, *Orthidæ*, and *Productidæ*, exist at the present day, but they are also represented in the older palæozoic epochs, and *Lingulæ* are among the oldest known fossils.†

The MOLLUSCA.—The term *Mollusca* may be used as a convenient denomination for the *Lamellibranchiata* and *Odontophora* (= *Gasteropoda*, *Pteropoda*, and *Cephalopoda*, of Cuvier), which can be readily shown to be modifications of one fundamental plan of structure. This may be represented by a body, symmetrical in relation to a median vertical plane, at one end of which is the oral, and at the other the anal aperture of the alimentary canal. In the body a ventral, or *neural*, face, an opposite dorsal, or *hæmal*, face, and a right and left side may be distinguished. The neural face usually gives rise to a muscular *foot*. The integument of the hæmal face is generally produced at its

'Trans. Royal Irish Academy,' 1869.

* Suess, "Ueber die Wohnsitze der Brachiopoden" ('Sitzb. d. Wiener Akad.,' 1857).

† See Davidson's 'Monographs of British Fossil Brachiopoda,' in the Palæontographical Society's publications.

edges into a free fold, and the term mantle, or *pallium*, is applied to the region of the integument thus circumscribed. Between the free portion of the mantle and the rest of the body is a cavity, the *pallial* chamber, from the walls of which, processes which subserve respiration, the *branchiæ*, may be developed.

In the median line of the surface of the mantle of the embryo, a *shell gland* is very generally formed, and from the surface of the mantle a cuticular secretion, the *shell*, is produced.

A systemic heart usually exists, and when present, is situated in the middle of the posterior hæmal region, and consists of, at fewest, two chambers, an auricle and a ventricle. Arterial vessels often ramify extensively through the body, but more or fewer of the venous channels remain in the condition of lacunæ. The blood corpuscles are colourless and nucleated. Distinct respiratory organs may be absent, or they may take the form of branchiæ or pulmonary sacs. When present, they lie in the course of the blood which is returning to the heart. Beside the heart and the intestine are situated the renal organs, which, on the one side, open externally, and on the other, communicate with the blood system.

The nervous system consists of, at least, one pair of ganglia (*cerebral*) at the sides, or on the hæmal aspect of, the mouth, and of two other pairs of œsophageal ganglia (*pedal* and *parieto-splanchnic*). The latter are situated at the sides, or on the neural aspect, of the alimentary canal, and are connected by commissures with the former.

In the majority of the *Mollusca*, the embryo passes through a stage in which it is provided with bands of cilia or with a simple, bifid, or multifid fold of the integument (*velum*), the edges of which are ciliated, developed on the hæmal aspect of the cephalic region of the body, in front of the pallial region.

The special peculiarities of the different groups of the *Mollusca* result chiefly—

1. From the form of the pallial region, and the extent of the mantle-lobes relatively to the body.

2. From the number and arrangement of the pieces of the shell to which the mantle gives rise.
3. From the proportional size and the form of the foot and the production, or non-production, of chitinous, or shelly, matter by it.
4. From the development of sense-organs on the anterior end of the body, and the absence or presence of a distinguishable head.
5. From the disproportionate growth of the hæmal region of the body into a *visceral sac*, followed by a change in the primitive direction of the intestine, and often accompanied by asymmetrical lateral distortion.

The LAMELLIBRANCHIATA.*—In these Mollusks there are always two large pallial lobes, the margins of which are devoid of setæ; and which are lateral, or right and left, in relation to the median plane. Each lobe gives rise to a piece, or *valve*, of the shell; and to these, accessory pieces, developed upon the median hæmal face (*Pholas*) or the posterior end of the mantle (*Teredo*), are in some cases added; or, in addition to its valves, the mantle may secrete a shelly tube (*Teredo, Aspergillum*). The shell itself consists of superimposed lamellæ of organic matter, hardened by the deposit of calcareous salts. It is a cuticular excretion from the surface of the mantle, and never presents any cellular structure. But from the disposition of its lamellæ, and from the manner in which the calcareous deposit takes place in them, it may present varieties of structure which have been distinguished as nacreous, prismatic, and epidermic.†

The two valves are generally united over the median line of the hæmal surface of the body by an uncalcified chitinous cuticular matter, termed the *ligament*, which is usually very elastic, and is so disposed, that, when the valves are closed, it is either stretched or compressed. In either case, it an-

* For a description of the anatomy of a Lamellibranch in detail, the student is referred to Huxley and Martin, 'Elementary Biology,' and Rolleston, 'Forms of Animal Life.'

† See Carpenter, article "Shell," Todd's 'Cyclopædia.' Huxley, "Tegumentary Organs," ibid.

tagonises the action of the adductor muscles and divaricates the valves when these muscles are relaxed. Conchologists commonly draw a distinction between an internal and an external ligament; but, in relation to the body of the animal, all ligaments are external, and their internality or externality is in respect of the *hinge line*, or the line along which the edges of the valves meet. In symmetrical, or *equivalve*, Lamellibranchs, each valve is concave internally and convex externally; it has, in fact, the form of a very depressed cone, the apex of which, termed the *umbo*, is incurved and is situated on, or projects beyond, the hæmal, or as it is termed, dorsal edge of the valve. Moreover it is usually inclined forwards, and situated nearer the anterior than the posterior end of the valve. Sometimes the umbonic cone is prolonged and bent inwards, or may even form a short spiral turn (*Isocardia*, *Diceras*), so that the valve acquires a certain resemblance to the shell of some gasteropods. As the shell of a Lamellibranch increases in thickness by the deposition of new layers on the interior face of the old ones; and, in area, by the extension of the new layers beyond the old ones, the summit of the umbo represents the original shell of the embryo, and the outer surface is usually marked by concentric *lines of growth*, which indicate the boundaries of the successively added new layers of shell substance.

The applied edges of the two valves are very often produced into elevations and depressions which interlock with one another. The form and arrangement of these teeth and sockets are of much use in systematic conchology.

The muscles which are attached to the valves, viz., the adductors, retractors of the foot and pallial muscles, give rise to impressions on the inner faces of the valves, which are very obvious when the latter are removed and cleaned. With the growth of the animal, the distance of these impressions from the hinge line and from one another is necessarily increased, and it is not difficult in some cases (*e.g. Anodonta*) to trace a faint triangular mark, which has its base in each adductor impression and its apex in the umbo,

and which indicates the successive shiftings of position of the muscle.

Fig. 117.

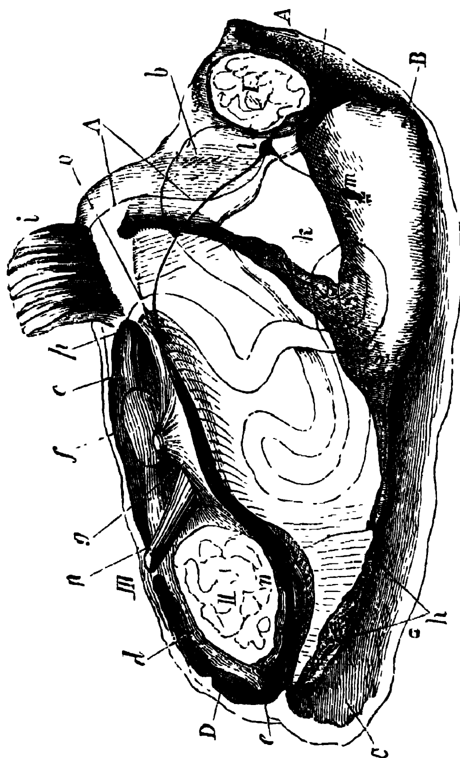


Fig. 117.—Sectional diagram of a freshwater Mussel (*Anodonta*).—A A, mantle, the right lobe of which is cut away; B, foot; C, branchial chamber of the mantle cavity; D, anal chamber; I, anterior adductor muscle; II, posterior adductor muscle; III, retractor muscle of the foot; *a*, mouth; *b*, stomach; *c*, intestine, the turns of which are supposed to be seen through the side walls of the mesosoma; *d*, rectum; *e*, anus; *f*, ventricle; *g*, auricle; *h*, gills, except *i*, right external gill, largely cut away and turned back; *k*, labial palpi; *l*, cerebral; *m*, pedal; *n*, parieto-splanchnic ganglia; *o*, aperture of the kidney or organ of Bojanus; *p*, pericardium.

In some cases (*e.g. Lima*) a Lamellibranch may perform a sort of aquatic flight by the flapping of the valves of its shell.

The hard and sharp edged valves of the shell in *Teredo* are probably the agents by which the mollusk carves its passages through the wood which it inhabits. Whether the valves of the shell of the *Pholades* and *Saxicavæ* are the instruments by which they excavate their burrows in hard rock, or whether, as has been suggested, the foot, armed with sand, is the boring instrument, is a question which has been much discussed, but hardly brought to a satisfactory decision.

The hæmal face of the body is either flat or slightly arched, whence, in side view, the hæmal contour is either straight or convex. In most Lamellibranchs, the body is symmetrical in relation to the median plane, but in those which have inequivalve shells, as the Scallop (*Pecten*) and the Oyster (*Ostræa*), the one half is more convex than the other. No Lamellibranch has a distinct head; but in those which possess two adductor muscles (*e.g. Anodonta*), the region in which the anterior adductor lies and which is situated in front of the mouth, may be distinguished as the *prosoma,* from the middle region (*mesosoma*) which gives rise to the foot; while the part which lies behind the foot and contains the posterior adductor may be termed the *metasoma.*

The foot may be rudimentary, but it is usually large, flexible, and employed as an organ of locomotion. The posterior face of the foot not uncommonly presents a gland which secretes a chitinous, or shelly, substance—the *byssus.*

From the sides of the mesosoma, close to the attachment of each mantle-lobe, the branchiæ project into the pallial cavity.

In its simplest form, the branchia of a Lamellibranch consists of a stem fringed by a double series of filaments (*e.g. Nucula*). The next degree of complication arises from these filaments becoming as it were doubled upon themselves at their free ends, the reflected portions lying on the

outer side of the outer, and on the inner side of the inner, series of primary filaments. But the free, or hæmal, ends of the reflected filaments contract no adhesion either with the mantle on the outer side, or with those of the opposite gill on the inner side. Delicate bands stretch from the primary to the reflected filaments across the interspace which they enclose (*Mytilus, Pecten*). In most Lamellibranchs, the gills are four elongated plates, each of which is in fact a long and narrow pouch, with its open end turned towards the hæmal face of the body. Two pouches are situated on each side of the mesosoma; one of these pouches is internal, the other external.* Their walls are united by transverse septa; they are richly ciliated, and are perforated by numerous apertures. As the outer wall of each pouch is united with the mantle, and the inner with its fellow of the opposite side, behind the foot, the whole branchial apparatus forms a sieve-like partition extended between the mantle and the foot (Fig. 117), and thus divides the pallial cavity into a *supra-branchial* and an *infra-branchial* chamber. Inasmuch as the hæmal edge of the inner wall of each inner branchial pouch is, for the greater part of its extent, not united with the mesosoma, but only closely applied against the latter, the supra-branchial and infra-branchial chambers may communicate by the cleft thus formed, as well as by the apertures in the lamellar walls of the branchial pouches. The anterior part of the supra-branchial chamber is divided into a right and left cavity by the interposition of the mesosoma, on the sides of which the apertures of the renal and generative organs are situated. The products of these organs therefore readily pass into these right and left cavities. The posterior part of the supra-branchial chamber, into which these two lateral divisions open, contains the termination of the rectum, and receives the fæces, as well as the urinary and generative products: it is therefore a sort of cloaca. Its external opening is usually termed the *anal opening* of

* The external gill pouch is often smaller than the internal. In species of *Lucina*, *Cytherea*, and *Tellina* only one gill pouch, the internal, is present.

the mantle cavity. The margins of this opening may be produced into a tube which is termed the *anal siphon.* In front of the anal, or rather cloacal, opening, the margins of the mantle may be completely disunited. Very frequently, however, they are conjoined, so as to leave only an opening for the exit of the foot, and another behind this, which is termed the branchial opening. The edges of this aperture may be prolonged into a tube, which is termed the *branchial siphon.* When a Lamellibranch is in its natural element and undisturbed, the valves of the shell gape sufficiently to allow of the free entrance or exit of water, to or from the pallial cavity; or, when siphons exist, they are fully protruded. The cilia with which the branchiæ are beset, work in such a manner as to drive the water from the infra-branchial chamber, through the openings of the branchiæ, into the supra-branchial chamber. From hence its only way of exit is by the cloaca and the anal siphon, when the latter exists. In order to make up for the water thus driven out, a new supply of water enters by the interspace between the lobes of the mantle, which bound the infra-branchial chamber, or by the branchial siphon. These currents may readily be made obvious by allowing a stream of finely-divided colouring matter to pass slowly towards the branchial siphon of a Lamellibranch. It will be seen to be swiftly sucked in, and after a very short time a coloured stream will flow out of the anal siphon. The same agency brings the nutritive matters suspended in the water within reach of the labial palpi, by which they are guided to the mouth.

Whatever form the branchiæ may possess, they are supported by a chitinous skeleton, in the form of a partial or complete investment to the transverse branchial vessels.

The mouth is bounded by lips, the angles of which are usually produced on each side into two *labial palpi.* Sometimes the lips are represented by a circular fold produced into numerous tentacula (*Pecten*). There are no organs for the prehension or mastication of food. A wide and short gullet leads into a stomach surrounded by the liver, which

consists of numerous cæca united into ducts which open into the stomach. Very generally a diverticulum of the pyloric end of the stomach contains a transparent rod-like body—the *crystalline style.*

The intestine usually makes many convolutions, but, finally reaching the middle line of the dorsal region of the body, it terminates by the anus in the posterior part of the pallial chamber. The heart lies in the region traversed by the termination of the intestine. It consists of an auricle and a ventricle, or of a ventricle and two auricles, or may be divided into two separate auricles and ventricles (*Arca*). Aortic trunks distribute the colourless blood to the body, whence it is carried to a large median venous sinus; from this it passes through the walls of the renal organs to the gills, and is returned from these to the auricular division of the heart.* Very generally the ventricle invests the rectum, but in *Ostræa, Teredo,* and *Anomia* the ventricle is quite detached from the intestine.

The renal organs, or *organs of Bojanus,* are usually two in number, often more or less united together, of a dark colour, situated beneath and behind the pericardium and in front of the posterior adductor muscle, extending forwards on each side of the mesosoma, and traversed by such numerous blood-channels that they have a spongy texture. The walls of the cavernous blood sinuses are lined with cells which secrete the urinary matters from the blood. These take the form of calcareous concretions containing uric acid. The gland communicates at one extremity with the pericardium; at the other, it either opens directly on to the surface of the body, or into a vestibular cavity which has an external aperture.

In *Ostræa* and *Teredo* the renal organ seems to be present in only a very rudimentary form.†

The mesodermal region, between the endoderm and the

* The circulatory organs of the freshwater Mussel have been very fully described by Langer. ('Denkschriften der Wiss. Akademie,' 1855 and 1856.)

† See for the structure of the renal organs and many other points connected with the ana-

ectoderm, is for the most part occupied by vascular, connective, and muscular tissues, and by the reproductive organs, so that there is no large perivisceral space. But there is—1. The large median sinus already mentioned, which receives the blood returned from all parts of the body, and is commonly termed the *vena cava*. 2. A spacious pericardial chamber which encloses the heart. It is in

Fig. 118.

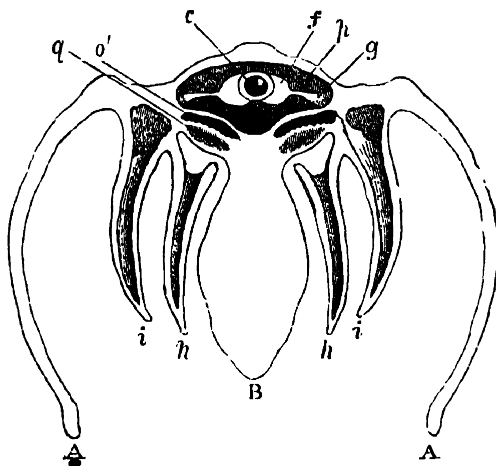


Fig. 118.—*Anodonta.*—Vertical and transverse section of the body through the heart; *f*, ventricle; *g*, auricles; *c*, rectum; *p*, pericardium; *h*, inner, *i*, outer gill; *o'* vestibule of *q*, the organ of Bojanus; B, foot, A A, mantle lobes

communication with the venous system, and, consequently, directly, or indirectly, with the vena cava. 3. The cavities of the renal organs, which usually freely communicate with

tomy of the *Lamellibranchiata*, the series of valuable papers of Lacaze-Duthiers. ('Annales des Sciences Naturelles, 1854 to 1861.')

one another, while they open into the pericardium on the one hand, and on the exterior of the body on the other. 4. In some *Lamellibranchiata*, canals open on the exterior of the body, especially on the surface of the foot. In this way the blood system is placed in direct, though circuitous communication with the surrounding water. These so-called *water-vessels* communicate internally with the venous system, of which, indeed, they seem to form a part. It is probable that all these cavities, taken together, represent the perivisceral cavity, pallial sinuses, and pseudo-hearts of a Brachiopod.

Strong bundles of muscular fibres, usually unstriated, pass transversely from one valve of the shell to the other, and bring them together; while they are divaricated by the elastic reaction of the ligament. Of such *adductor* muscles there may be either one or two. When there are two (*Dimyaria*), the *anterior adductor* lies in front, and on the hæmal side of, the œsophagus; while the *posterior adductor* lies in front, but on the neural side, of the rectum. Hence the alimentary canal, as a whole, lies between these two muscles. When only one adductor muscle exists (*Monomyaria*), it is the posterior.

The foot is retracted between the valves of the shell by two or three pairs of retractor muscles, of which the anterior and posterior pairs are usually attached to the shell, close to the anterior and posterior adductor impressions. The protraction of the foot appears to be effected by the compression of the blood by the intrinsic muscles of the walls of the mesosoma and of the foot itself.

Each lobe of the mantle is attached to the corresponding valve of the shell by a series of muscular fibres, the attachments of which give rise to a linear impression, which runs from one adductor to the other, and constitutes the *pallial line*. When the siphons are largely developed they have retractor muscles, the insertions of which are so disposed as to cause the posterior part of the pallial line to be more or less deeply curved or angulated. Hence the distinction of

integropalliate and *sinupalliate* as applied to Lamellibranchs which have the pallial line evenly rounded or notched.

The *cerebral ganglia* lie at the sides of the mouth, and are connected by a commissure, which passes in front of it. They give branches to the anterior region of the mantle, to the gills, to the anterior adductor muscle, to the labial palpi, and to the parts about the mouth. The *pedal ganglia* are situated in the foot; or in the corresponding region on the neural side of the alimentary canal, when no foot is developed. Each is united by a commissure with the cerebral ganglion of the same side, and gives off branches to the muscles of the foot. The *parieto-splanchnic* ganglia lie on the neural face of the posterior adductor muscle. The long commissures which unite them with the cerebral ganglia usually traverse the renal organ, and lie beneath the floor of the pericardium. Each of these ganglia gives off a nerve to the branchia of its side, and supplies the posterior and middle part of the mantle. This posterior pallial nerve may anastomose with the anterior pallial nerve from the cerebral ganglion. The ganglia also furnish nerves to the posterior adductor muscle, to the heart, to the rectum, and to the muscles of the siphons, when the latter are present. Eyes are never developed in the cephalic region of the Lamellibranchs, but, in many (*e.g. Pecten*) numerous simple eyes terminate papillæ of the margins of the mantle. Auditory sacs are almost invariably attached by longer or shorter peduncles to the pedal ganglia.

The *Lamellibranchiata* are usually diœcious, but sometimes hermaphrodite* (*e.g. Cyclas*, some species of *Cardium* and *Pecten*, *Ostræa*, *Clavagella* and *Pandora*). The genera-

* The testes and ovaria are distinct in the hermaphrodite *Pectines*. In *Cardium serratum*, adjacent cæca of the sexual gland contain spermatozoa or ova, or both products may be developed in the same cæcum. In the common Oyster the genital cæca in any given individual are found to be either almost all ovigerous or almost all spermigerous; and it appears probable that the predominantly male, precedes the predominantly female, condition. See Lacaze-Duthiers, "Organes génitaux des Acéphales Lamellibranches" ('Ann. des Sciences Naturelles,' 1854).

tive organs are ramified glands of simple structure and similar in both sexes, the ducts of which open into, or close to, the renal organs.

The process of yelk-division * usually gives rise to smaller and larger blastomeres, of which the former, as an epiblast, invest the latter as a hypoblast. At the cephalic end of the embryo of most Lamellibranchs, a velum, or disk with richly ciliated edges and, usually, a central tuft of longer cilia, is formed. On the dorsal face of the embryo the integument rises into a patch with raised edges, which is the rudiment of the mantle. The separation of the shell into two valves, united by an uncalcified hinge, must probably be ascribed to the manner in which the calcareous matter subsequently added to the shell is deposited. The foot appears as a median outgrowth of the neural face of the embryo behind the mouth. The branchiæ have, at first, the form of separate filamentous processes, which are developed from the roof of the anterior part of the pallial cavity, at the point of junction of the mantle with the mesosoma, and gradually increase in number from before backwards. In those Lamellibranchs which have pouchlike gills, it appears that the processes which are first formed become the outer lamella of the inner gill-plate, their free ends uniting together; the inner lamella of this plate is produced by the upgrowth of a thin lamina, which subsequently becomes perforated, from the united ends of these processes. The inner lamella of the outer gill is formed of branchial processes, which grow out from the attached ends of the first set; and the outer lamella of this gill is produced in the same fashion as the inner lamella of the inner gill.†

Recent observations tend to show that in these, as in other *Invertebrata*, the nervous ganglia are modified ingrowths of the epiblast.

* See Lovén, 'Archiv für Naturgeschichte,' 1849. De Quatrefages, "Mémoires sur l'Embryogénie des Tarets" ('Ann. des Sc. Nat.,' 1849).

† Lacaze-Duthiers, "Sur le développement des branchies des Mollusques acéphales Lamellibranches" ('Ann. des Sciences Naturelles,' 4, iv.).

The simplest form of development of the *Lamellibranchiata* has been observed in *Pisidium*.* By the process of cleavage, the vitellus is divided into a number of equal blastomeres. The morula thus formed undergoes invagination, and is converted into a gastrula. The blastopore, or aperture of invagination, closes, and the epiblast, or ectodermal layer of the embryo, growing much faster than the hypoblast, or endodermal layer, the latter forms a small shut sac, the primitive alimentary sac (or *archenteron*) attached to one point of the inner surface of the much larger ectodermal sac. The mesoblastic cells appear to be derived both from the epiblast and the hypoblast.

The mouth is formed by a depression of the ectoderm at the anterior end of the body, which grows towards and opens into the archenteron. The anus is developed at the opposite end, in the region of the primitive invagination. On the neural face of the embryo, the foot grows out, while the mantle appears on the opposite face; and, in the centre of the mantle, a transversely oblong depression lined by elongated cells is the 'shell gland.' In the median line this answers to the ligament, and, at the sides, to the middle region of the future valves of the shell; but the precise share, if any, which it takes in the formation of these parts does not appear. *Pisidium* has no velum.

The development of one of the fresh-water Mussels (*Unio pictorum*) has recently been worked out very fully by Rabl.† The vitellus divides into two unequal masses, of which the larger is termed by Rabl the 'vegetative' and the smaller the 'animal' cell, somewhat inconvenient names which may be replaced by '*macromere*' and '*micromere*.' Each of these becomes subdivided, partly by ordinary fission, partly, as in the case of the macromere, by a process of budding, into blastomeres, of which those which proceed from the macromere long remain larger and more granular than those which proceed from the micromere. The blastomeres

* Lankester "On the Developmental History of the Mollusca." ('Phil. Trans.' 1874.)

† C. Rabl, 'Ueber die Entwickelungsgeschichte der Malermuschel,' Jena, 1876.

arrange themselves into a hollow sphere—the *blastosphere*. This is a vesicular morula, composed of a single layer of blastomeres, of which those of one hemisphere have proceeded from the micromere, and those of the other from the macromere. Two blastomeres of the macromeral hemisphere remain much larger than the rest. The macromeral hemisphere next undergoes invagination, and its invaginated part becomes the hypoblast. The two large blastomeres just mentioned, which are disposed symmetrically, one on each side of the median plane at the anterior margin of the area of invagination, become enclosed between the hypoblast and the epiblast, and by their division give rise to the mesoblast. This last, therefore, may be regarded as an indirect product of the hypoblast.

The endodermal sac formed by the hypoblast now loses its connection with the region of the embryo of which it is an invagination, and applies itself to the anterior wall of the body, where an involution of the ectoderm, which gives rise to the oral cavity, takes place. The greater part of the mesoblastic cells become the adductor muscle, which is at first single and answers to the posterior adductor of the adult. There seems to be no shell gland. The shell appears at first as a membranous cuticula, continuous from side to side, and therefore undivided into two valves. Subsequently it becomes calcified and bivalve. The byssus gland is developed as an involution of the ectoderm at the posterior end of the body; and the ventral hemisphere, or that opposite the shell, becomes divided by a deep median fold into the two lobes of the mantle on which the characteristic pencil-like papillæ appear. In front of the rudimentary mouth are two ciliated depressions of the ectoderm, which are possibly the rudiments of the nervous ganglia.

In *Unio* and *Anodonta* the young are hatched in the outer gill pouches of the parent, from which they are so dissimilar that they were at one time considered to be parasites (*Glochidium*). The valves of the shell are triangular and have incurved and serrated apices, by the help of which the larvæ, after they leave the parent, attach themselves to

fishes and other floating bodies. In this position they undergo a sort of metamorphosis, and eventually fall off and sink to the bottom as minute fresh-water Mussels.

On comparing the *Lamellibranchiata* with the *Brachiopoda*, it is obvious that the two have, in common with one another and with the *Annelida*, the ciliated or veligerous larval form. If the shell gland is, as Mr. Lankester suggests, the homologue of the peduncular gland of *Loxosoma* and of the Brachiopod larvæ, it follows that the peduncle of the Brachiopod corresponds with the centre of the pallial surface of the Lamellibranch, and that the so-called dorsal and ventral lobes of the mantle in the Brachiopod correspond with the anterior and posterior halves of the mantle in the Lamellibranch. The Brachiopod hinge will therefore be transverse to the axis of the body, while the Lamellibranch hinge is parallel with it. If this comparison be just, however, the three segments of the Brachiopod larva cannot answer to the segments of an Annelid larva, but the two posterior segments of the Brachiopod larva must represent an outgrowth of the hæmal side of the body; and this would correspond very well with the arrangement of the intestine in the articulated *Brachiopoda*.

In the simplest forms of the *Lamellibranchiata*, as *Trigonia*, *Nucula*, and *Pecten*, the mantle-lobes are almost, or completely, disunited with one another and with the branchiæ, and the latter are either simple plumes or have undergone but little modification. The hæmal face of the body is short relatively to its vertical height.

In most Lamellibranchs the hæmal face of the body is longer; the gills are lamellar, and the mantle-lobes are united with one another and with the gills, so as to separate a supra-branchial from an infra-branchial chamber (*Anodonta*). In yet others, the posterior margins of the mantle are produced backwards into short *siphons*, but the mantle-lobes remain separate for the rest of their extent (*Cardium*); in others, the siphons are greatly elongated and the ventral margins of the mantle-lobes unite, so as to leave only a small median aperture for the foot (*Pholas*). In the

most modified forms, the body becomes more and more elongated, until, in *Teredo*, it is completely vermiform, and the valves of the shell cover but a very small portion of the body.

The foot is wanting as a distinct structure in *Ostræa*; while in *Cardium* and *Trigonia* it is a large muscular organ, by the aid of which the animal is able to leap for some distance. The byssus may be present in the young and absent in the adult (*e.g. Anodonta*). It may have the form of strong chitinous filaments (*Mytilus*) or of a plate of horny or shelly texture (*Arca, Anomia*). The inequality of the valves attains its maximum in the *Hippuritidæ*, in which one valve may have the form of a long cylinder, or cone, while the other is a flattened plate.*

The shells of Lamellibranchs are among the most abundant of fossil remains in all epochs of the world's history. In the Palæozoic formations, however, the proportion of these mollusks relatively to the *Brachiopoda* is the reverse of what obtains at the present day, the latter being very numerous, while the Lamellibranchs are comparatively scanty. The integropalliate are far more numerous than the sinupalliate forms in the older rocks. The *Hippuritidæ* of the Cretaceous epoch is the only family of ancient Lamellibranchs which is extinct at the present day; and the only one which diverges to any considerable degree from existing forms.

The ODONTOPHORA.—In the Mollusks which belong to this division, the mantle, always present in the newly hatched young, may abort in the adult condition. It is never divided into two lobes, though it may be slit or perforated where it forms the wall of the branchial chamber (*Haliotis, Fissurella*).

Very generally, the prosoma bears tentacula and eyes; and a distinct head being thus recognisable, these Mollusks

* For an excellent account of the *Lamellibranchiata* from the conchological side, see Woodward's 'Manual of the Mollusca.'

have been named *Cephalophora*, in contradistinction to the acephalous Lamellibranchs and Brachiopods.

The mantle commonly gives rise to a shell; which may either be a more or less calcified cuticular product of the epidermis, covering the outer surface of the mantle, when it constitutes an external shell, as in the *Lamellibranchiata* and *Brachiopoda*; or it may be developed within a sac in the interior of the mantle, as an internal shell. In neither of these cases is it ever a bivalve shell divided into two lateral portions.* Usually it is in one piece (univalve), but in one group, the *Chitonidæ*, it consists of a number of pieces (not exceeding eight), arranged in longitudinal series along the middle line.

Calcareous matter is very commonly diffused, in the form of granules, through the connective tissue, and often takes the form of spicula (*e.g. Doris*).

The mesosoma is generally prolonged into a muscular foot, which may be provided with lateral appendages, the *epipodia*. And, on the hæmal aspect of the posterior portion of the foot, a chitinous or shelly plate, termed the *operculum*, may be developed. This operculum appears to be the analogue, if not the homologue, of the byssus of the Lamellibranchs; and is certainly not homologous with either of the valves of the shell of the latter, which are pallial structures. The edge of the mantle forms a free fold which nearly or entirely surrounds the mesosoma; and in one genus, *Dentalium*, the margins of the mantle unite for the greater part of their length: in all the rest they remain free. A space is enclosed between the lobes of the mantle and the mesosoma. Usually this space is much larger on one face of the body, and constitutes the pallial chamber. As a rule, the branchiæ are lodged in this chamber, and the anus opens into it.

In a very few *Odontophora*, the symmetry of the body is

* The singular bivalve plates, termed *Aptychus*, which occur in the *Ammonitidæ*, whatever their nature may be, are obviously not homologous with the shell of ordinary Mollusks, which is represented by the chambered shell of the cephalopod.

undisturbed; that is to say, the mouth and the anus are situated at opposite ends of the axis of the body, and the hæmal face is not produced into a visceral sac (*e.g. Chiton, Dentalium*). But, in the great majority, such a visceral sac is formed. In the *Cephalopoda*, it co-exists with bilateral symmetry, inasmuch as the mantle and the anus lie in the plane which divides the body into two similar halves. But, in most *Odontophora*, the anus is twisted to one side (usually the right), and in many, it is situated, together with the pallial chamber in which it is contained, on the anterior face of the body.

The mouth lies at the anterior end of the body, on the hæmal side of the anterior part of the foot (except in the *Cephalopoda*). It may be provided with variously disposed jaws, or cutting plates, of a chitinous or calcified substance. But the structure which is most characteristic of the *Odontophora*, and which is absent in only very few genera (*e.g. Tethys, Doridium, Rhodope*), is a peculiar rasping and sometimes prehensile apparatus, the *odontophore*, or as it is often termed, the tongue, which is attached to the floor of the mouth (Fig. 119, 120).

This apparatus consists of a *skeleton*; of a *subradular membrane*, which is continuous with the lining of the oral cavity; of the *radula*; and of *intrinsic* and *extrinsic muscles*.

The skeleton is composed of two principal masses of partially fibrous, or completely cartilaginous tissue (*odontophoral cartilages*), which may be more or less confluent, and are further united together in the middle line by fibrous and muscular tissue. Their anterior ends and oral faces are free and smooth, and are usually excavated so as to present a trough-like surface to the subradular membrane, which rests upon them. Accessory cartilages may be added to these. Behind, the subradular membrane is continued into a longer or shorter sac, lined by a continuation of the buccal epithelium. The radula is a cuticular chitinous product of the epithelium of the subradular membrane. It is armed with tooth-like processes arranged in one or many series; and additions are constantly being made to its pos-

terior end, which is lodged in the sac of the subradular membrane. Thus the teeth are replaced from behind, as fast as they are worn away by friction against the food which they rasp, at the anterior end of the ribbon.

The intrinsic muscles of the odontophore are attached, on

Fig. 119.

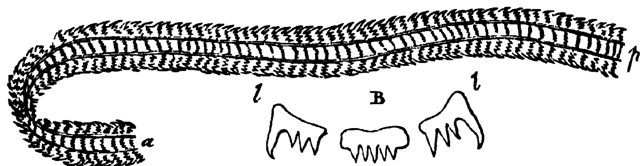


Fig. 119.—*Buccinum undatum.*—A, radula; B, one of the transverse rows of teeth. *a*, anterior, *b*, posterior end; *c*, central, *l*, lateral teeth. (After Woodward, 'Manual of the Mollusca.')

Fig. 120.

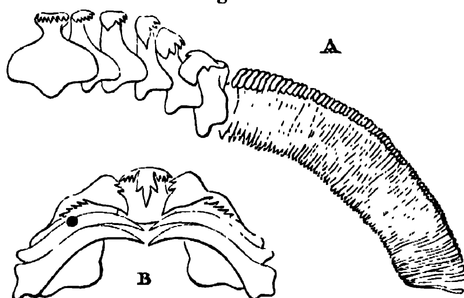


Fig. 120.—A, *Trochus cinerarius;* the median tooth and the teeth of the right half of one row of the radula. B, *Cypræa Europæa*, one row of teeth of the radula. (Woodward, ibid.)

the one hand, to the posterior and under faces of the odontophoral cartilages, and, on the other, to the subradular membrane, some being inserted into its posterior and lateral portions, and others into its anterior extremity, after it has turned over the anterior extremities of the principal cartilages. Certain of the muscular bundles are also

attached to the fore part of the odontophoral cartilages themselves. The contraction of these muscles must tend to cause the subradular membrane, and with it the radula, to travel backwards and forwards over the ends of the cartilages in the fashion of a chain-saw, and thus to rasp any body against which the teeth may be applied. When undisturbed, the radula is concave from side to side, and the teeth of the lateral series, being perpendicular to the surface to which they are attached, are inclined inwards towards one another. But when the intrinsic muscles come into action, the radula, as it passes over the ends of the cartilages, becomes flattened, and the lateral teeth are consequently erected or divaricated. The extrinsic muscles pass from the odontophore to the lateral walls of the head, and protract or retract the whole apparatus. They may give the protruded extremity of the radula a licking motion, which is quite independent of the chain-saw action due to the intrinsic muscles.*

The odontophore is developed very early, and it would be interesting to know whether it exists in the young of those few *Odontophora*, in which it is wanting in the adult state.

Salivary glands are very generally present in the *Odontophora*,† and the liver is usually large.

As in the Mollusca in general, the blood corpuscles are

* In my memoir "On the morphology of the Cephalous Mollusca" (Phil. Trans. 1852), I described the chain-saw action of the odontophore, as I observed it in the transparent *Firoloides* and *Atlanta*, while living. But as Troschel has remarked in his excellent monograph ('Das Gebiss der Schnecken,' erste Lieferung, pp. 19, 20, 1856), I did not sufficiently dwell on the frequency and importance of the licking action produced by the extrinsic muscles. I am still of opinion, however, that this action cannot be rightly described, as a movement of the radula following secondarily upon that of the cartilages, inasmuch as it is a motion of the whole odontophore. On the other hand, it may be, as has been suggested to me by Mr. Geddes, who at my suggestion has undertaken a re-examination of the structure of the odontophore, that the flexure of the anterior ends of the odontophoral cartilages, by the intrinsic muscles inserted into them, plays an important part in the motion of the radula.

† In *Dolium* the salivary secretion contains free sulphuric acid.

colourless and nucleated. The blood plasma is red in *Planorbis.*

The heart may be wanting (*Dentalium*) or it may resemble that of the Lamellibranchs in having two auricles (*Chiton, Haliotis*), and even in being perforated by the rectum (*Haliotis, Turbo, Nerita*); most commonly it consists of a single auricle and a single ventricle. In the Cephalopods, it is hard to say whether the two or four branchio-cardiac trunks which open into the ventricle should be regarded as veins or as auricles. An accessory "portal" heart has been described in *Doris.** Special respiratory organs may be wanting, their place being taken by processes of the body, or by the walls of the mantle cavity, or by the general surface.

The branchiæ, when present, are numerous lamellar processes, or from one to four plume-like gills. Aerial respiration is effected by the walls of a pulmonary sac, which is a modification of the pallial cavity.

The presence of renal organs, in the form of one or more sacs situated close to the heart, open to the exterior on one side and, on the other, in relation, usually by means of a glandular structure, with the returning current of blood, is very general; and, in many cases, these renal sacs communicate directly with the blood sinuses through the pericardium. In many Pteropods and Heteropods they are rhythmically contractile.

As in the *Lamellibranchiata*, so in many *Odontophora*, simple or branched canals traverse the substance of the foot and open externally by a more or less conspicuous pore, which is usually situated upon its inferior face. These *aquiferous canals*, as they have been termed, appear, in many cases, to open by their inner ends into the blood sinuses, and thus to establish a direct communication between the blood and the surrounding water. In species of *Pyrula*, Agassiz found that coloured fluids injected into the pore passed into and filled the blood vessels generally. But it

* Hancock and Embleton, "On the Anatomy of Doris." ('Phil. Trans.' 1852.)

may be doubted whether these canals should be regarded as a special system of vessels, rather than as blood sinuses which open externally.

The arrangement of the centres of the nervous system in *Dentalium* * most nearly approaches that which exists in the *Lamellibranchiata.* Two cerebral ganglia lie close together on the hæmal side of the œsophagus. A long commissural cord connects each of them with one of the pedal ganglia, which are also closely united. A second long commissure passes backwards from the cerebral ganglia, and often presents a ganglionic enlargement at its origin. It unites with one of two ganglia, situated close to the anus, and connected, in front of it, by a rather long transverse commissure. The nerves distributed to the posterior half of the mantle are given off from these ganglia, and those to its middle region from the anterior end of the commissure or its ganglionic enlargement. There seems no reason to doubt that the ganglia close to the anus, together with the ganglionic enlargements at the anterior ends of the commissures which connect them with the cerebral ganglia, correspond with the parieto-splanchnic ganglia of the Lamellibranchs, and that the cerebral and pedal ganglia are the homologues of those so named in the latter Mollusks.

In addition to this approximation of part of the ganglionic mass of the parieto-splanchnic system to the cerebral ganglia, *Dentalium* differs from the Lamellibranchs and resembles other *Odontophora*, in the possession of a system of *buccal* nerves, which arise from the cerebral ganglia, and in which minute ganglia are developed. The nerves which proceed from the buccal ganglia are distributed to the odontophore and its muscles.

In other *Odontophora*, the two cerebral and two pedal ganglia, with their commissures, are always to be recognised; but the number of the ganglia which represent the parieto-splanchnic system may be increased, and the anterior ganglia of this system may attain a large size, and may

* See Lacaze-Duthiers, 'Organisation du Dentale.'

come into close relation not only with the cerebral but with the pedal ganglia.

In *Lymnœus palustris*,* for example, there are five such ganglia situated close to the cerebro-pedal ring. The most anterior of these, on each side, is united with both the cerebral and the pedal ganglion of its side; and appears, indeed, like an enlargement upon a second commissure between those two ganglia. The ganglia which constitute the second pair are united, in front, by a short commissure, with the preceding; and, behind, with the fifth or azygos ganglion. The second pair of ganglia give off the nerves to the right and left sides of the mantle respectively.

In *Limax*, and apparently in the terrestrial *Pulmonata* generally, the arrangement is essentially the same, except that all the ganglia of the parieto-splanchnic system coalesce into one mass; between which and the pedal ganglia, the aorta passes.

In *Haliotis*,† on the other hand, while the anterior parieto-splanchnic ganglia are situated close to the pedal ganglia and are connected with them and with the cerebral ganglia, in such a manner as to give rise to an apparent second cerebro-pedal commissure, the ganglia which represent the second pair in *Lymnœus*, are situated at the base of the branchiæ and are united by a long commissure with one another, and also with the anterior parieto-splanchnic ganglia. Of the latter commissures, that from the left branchio-pallial ganglion goes to the right anterior parieto-splanchnic ganglion, and *vice versâ*.

With respect to the position of the cerebral and pedal ganglia in the *Odontophora*, the commonest arrangement is that in which the cerebral ganglia are supra-œsophagæal, and are connected by two longer or shorter commissures, on each side, with the pedal and anterior parieto-splanchnic

* Compare Lacaze-Duthiers, "Du système nerveux des Mollusques gastéropodes pulmonés aquatiques" ('Arch. de Zoologie,' 1872), and the numerous figures of the arrangement of the cerebral ganglia of the nervous system given in his memoir on the otocysts. (Ibid.)

† See Lacaze-Duthiers, "Sur le système nerveux de Haliotide."

ganglia, both of which are infra- or post-œsophagæal. But in many cases (most *Nudibranchiata*), the pedal and parieto-splanchnic ganglia are approximated to the cerebral ganglia (the latter being supra-œsophagæal), and are united by long sub-œsophagæal commissures. In others, as in most *Pteropoda*, the pedal and parieto-splanchnic ganglia are sub-œsophagæal; while the cerebral ganglia, brought close to them, are united by a supra-œsophagæal commissure.

Accessory ganglia are frequently developed in the region of the heart and branchiæ, on the nerves of the parieto-splanchnic system.

A complicated system of visceral nerves is distributed over the whole length of the alimentary canal, the genital organs, and various parts of the vascular system, in many *Odontophora*.*

Two auditory vesicles usually exist, and very generally appear to be sessile upon the pedal ganglia. In the *Heteropoda*, in many *Nudibranchiata*, as shown by Hancock, and in numerous genera of *Branchio-* and *Pulmo-gasteropoda*, which have been carefully examined by Lacaze-Duthiers,† however, there seems to be no doubt that the auditory nerves arise from the cerebral ganglia, even though the vesicles may be situated close to the pedal ganglia.

Olfactory organs certainly exist in the *Cephalopoda* in the form of saccular involutions of the integument near the eyes; and it is very probable that the integument of the

* See especially Hancock and Embleton, "The Anatomy of Doris" ('Phil. Trans.,' 1852).

† "Otocystes des Mollusques." ('Archives de Zoologie Expérimentale,' 1872.) In the memoir the origin of the acoustic nerves from the cerebral ganglia is determined in so many *Pulmogasteropoda* (*Limax*, *Arion*, *Testacella*, *Clausilia*, *Zonites*, *Helix*, *Succinea*, *Physa*, *Lymnæus*, *Ancylus*) and *Branchiogasteropoda*, (*Neritina*, *Paludina*, *Cyclostoma*, *Pileopsis*, *Calyptræa*, *Natica*, *Nassa*, *Trochus*, *Murex*, *Cassidaria*, *Purpura*, *Patella*, *Haliotis*, *Philine*, *Aplysia*, *Lamellaria*), that there is a large basis for the generalisation that this mode of origin is universal. Moreover, according to Lacaze-Duthiers, the same law holds good for the *Cephalopoda*. Such being the case, the question suggests itself whether the connexion of the nerves of the otocysts with the pedal ganglia, which obtains universally among the Lamellibranchs, indicates their real or only their apparent origin.

tentacula, or of the lips, may subserve the same function in the Gasteropods.

Eyes are generally present, and are limited to two, situated in the head. They resemble the vertebrate eye in structure, so far as they possess a concave retinal expansion and usually, in front of this, a vitreous humour, lens, and cornea. But they differ from the eyes of *Vertebrata*, and resemble those of other invertebrated animals, in that the structures which answer to the rods and cones are situated on that face of the retina which is turned towards the light, while the fibres of the optic nerve traverse the pigment layer to reach them.

The reproductive organs of the *Odontophora* present very great diversities of structure. They may be either diœcious or monœcious, and each type of reproductive organs may present various degrees of complexity. Of the diœcious reproductive organs, there are two chief forms; the one in which the duct of the ovarium or testis is continuous with the gland; and the other in which the duct opens into a sac, into which the ova or spermatozoa are set free by the dehiscence of the follicles in which they are developed. The latter arrangement is met with in the *Cephalopoda*; the former appears to prevail among all the other diœcious *Odontophora*.

In these, the racemose generative gland is usually situated close to the liver. In the female, the oviduct ordinarily presents a uterine dilatation towards its termination, which is generally situated in the pallial cavity on the right side of the body. In some rare cases (*Paludina, Neritina*), a dilatation or a special vesicular appendage of the uterus may serve as a *vesicula seminalis;* and, in *Paludina*, according to Leydig, an albumen gland opens into it.

A penis is not always present. When it exists, it is a muscular process of the mesosoma, to which the semen may be led from the opening of the vas deferens by a groove; or it may be traversed by the vas deferens which opens near, or at, its apex.

In all the monœcious *Odontophora* which have as yet

been thoroughly examined, there is a generative gland termed the *ovotestis*, in which both spermatozoa and ova are produced. Only in the anomalous genus *Rhodope*, (Kölliker), are the spermatozoa and ova formed in distinct cæca; in all the rest, each cæcum is, hermaphrodite, the spermatozoa and the ova being usually developed in different parts of the cæcum. The duct of the ovotestis may remain single to its termination at the genital aperture; or become only incompletely divided into two semicanals (*Pteropoda, Pleurophyllidia, Umbrella, Aplysia*); or it may become, at first, partially, and then completely, divided into an oviduct and a vas deferens (*Nudibranchiata, Pleurobranchia, Pulmonata*).

In the former case, there is but one genital aperture. The common duct usually receives the secretion of a uterine gland which may take the form of a special albumen gland, and a spermatheca opens into it near its outer extremity; while, on the male side, a vesicula seminalis, and an eversible penis may be added.—The penis, however, may be distant from the genital opening, and then a groove on the side of the body leads to it (*Aplysia*). In the latter case, there are two genital apertures, one for the male and one for the female organs, though they may open into a common vestibule. The penis is an eversible involution of the integument, on which the vas deferens opens. A prostate gland is usually connected with the latter, and, near its opening, there may be a saccular appendage, in which a hard pointed body, the *spiculum amoris*, is contained (*Doris, Helicidæ*). An albumen gland opens into the uterus, and a spermatheca is connected with the vagina.

Spermatophores, by the aid of which the spermatozoa are transferred into the female organs, occur in the *Cephalopoda*, and in the *Pulmonata*. In the latter they are grooved bands, or incomplete tubes of hardened mucus secreted by the penis, which become filled with spermatozoa during copulation; while, in the former, they are closed cases which may have a very complex structure.

In the great majority of the *Odontophora*, the young

leaves the egg as a *veliger* very similar to that of the *Lamellibranchiata*. The velum usually becomes bilobed, and sometimes (*Heteropoda*), its margins are produced into many tentaculiform processes; and, in all *Pteropoda* and *Branchiogasteropoda*, whether the adult possess a mantle and a shell or not, the larva is provided with both, the shell being at first a simple conical symmetrical cap, developed in the middle line of the mantle. The eyes make their appearance behind the velum, and the tentacles in front of or upon it.

While the course of the development of the embryo in the *Odontophora* presents a general uniformity, there are wide differences in detail.

In *Paludina*,* the blastomeres produced by yelk division are of equal size. They arrange themselves into a vesicular morula, which undergoes invagination and becomes a gastrula of the simplest type. The aperture of invagination (blastopore) becomes the anus, while the mouth is formed by an involution of the ectoderm of the anterior end of the body, which extends towards and eventually opens into, the blind end of the archenteron or primitive alimentary sac. A ciliated velum is developed on the hæmal side of the mouth; and a 'shell gland' appears in the centre of the area which gives rise to the mantle.

In *Lymnæus*,† also, cleavage ends in the production of blastomeres of equal size, whether with or without a transitory stage of inequality, and the vesicular morula undergoes invagination to give rise to the archenteron. The blastopore is elongated, and it appears to be likely that its anterior and posterior ends may coincide with, if they do not give rise to, the mouth and anus respectively.

In most *Odontophora*, the process of yelk division goes on unequally, and results in the production of large and small

* Lankester, "On the coincidence of the blastopore and anus in *Paludina vivipara*." ('Quarterly Journal of Microscopical Science,' 1876.)

† Lankester, "Observations on the development of the Pond Snail" ('Quarterly Journal of Microscopical Science,' 1874), and C. Rabl, "Die Ontogenie der Süsswasser Pulmonaten" ('Jen. Zeitschrift,' 1875).

blastomeres (macromeres and micromeres). The latter form a layer which gradually extends over the macromeres and encloses them. Obviously this comes to the same result as invagination; and the included macromeres and their progeny either become converted into the archenteron with its appendages, and more or less of the mesoblast; or a portion of them may serve as food yelk.

In the *Pteropoda* and *Heteropoda*,* and in *Nassa*, *Natica*, and *Fusus*,† the blastopore, or aperture circumscribed by the edges of the micromeral layer as it grows round the macromeres, closes, but corresponds in position to the invagination of the ectoderm which gives rise to the future mouth; and the anus is a new formation.

In such land *Pulmonata* as *Limax*, the process of yelk division gives rise to macromeres and micromeres, and the atter enclose the former. What becomes of the blastopore is not clear, though I am inclined to think that it corresponds in position with the mouth. The latter is seen very early as a funnel-shaped invagination of the epiblast bounded by lateral lips. Behind it, the foot grows out and rapidly attains a considerable size. Its posterior extremity becomes flattened from above downwards, and converted into an orbicular appendage, the opposite walls of which are connected by reticulated muscle-cells. This appendage undergoes rhythmical movements of dilatation and contractions. The macromeres form a large mass enclosed within a spheroidal dilatation of the greater part of the hæmal wall of the body, which deserves the name of yelk-sac even better than the structure so named in the *Cephalopoda*, inasmuch as it more nearly corresponds, morphologically, with the vitelline sac of vertebrated animals. Between this sac and the foot, the small remainder of the hæmal wall becomes converted into the mantle.

The walls of the vitelline sac undergo contractions which

* Fol, "Etudes sur le développement des Mollusques." ('Arch. de Zoologie expérimentale,' 1875, 1876.)

† Bobretsky, "Studien über die embryonale Entwickelung der Gastropoden." ('Archiv f. Mikr. Anat.,' 1876.)

sometimes, but not always, alternate with those of the pedal appendage. On each side of it appears the "primitive kidney," consisting of a curved elongated series of cells within which concretions are developed, and terminating in a duct which opens on the posterior face of the vitelline sac, close to the mantle. The exact mode of origin of the alimentary canal has not been made out; but, in any case, only a very small portion of the endodermal cells can take part in its formation, and the archenteron is, at first, a sac which nearly fills the small projection formed by the rudimentary mantle. The oral involution of the ectoderm gives rise to the odontophore, and extends across the base of the foot to open, eventually, into the archenteron.

The fold of the mantle which overhangs the respiratory aperture, makes its appearance very early; and immediately behind it, the intestine is visible as a short tube, which extends from the archenteron to the surface, but does not, at first, open there.

As development proceeds, a movement of the macromeric part of the vitellus takes place in exactly the opposite direction to that of the food yelk of the *Cephalopoda;* that is to say, from the vitelline sac into the constantly enlarging foot. The alimentary canal accompanies it, the anus alone remaining in its primitive position. The constantly lengthening alimentary canal becomes disposed in folds; between these the macromeric part of the vitellus, which gradually forsakes the diminishing vitelline sac, disposes itself around the coils of the intestine. Eventually, for the most part, it becomes converted into the liver.

The rudimentary shell first makes its appearance in the form of a few subcrystalline calcareous plates, on the inner side of the ectoderm.*

The development of *Helix* is similar to that of *Limax;* but the intestine passes into the large visceral sac instead of into the cavity of the mesosoma. The shell is stated by Gegenbaur to be at first internal, as in *Limax.* In neither

* Compare Gegenbaur, "Zur Entwickelungsgeschichte der Land-Gasteropoden." ('Zeitschrift für Wiss. Zoologie,' 1852.)

case, has the relation of the shell to the shell-gland been determined.

The process of development appears to present a considerable range of variation in the *Pulmonata*. Semper * states of a species of *Vaginulus*, that, after the process of cleavage, the embryo assumes the form of a cylinder, at one pole of which the rudiments of the tentacula and of the lips appear; while, at the sides, a longitudinal ridge indicates the edge of the mantle, and marks off the more convex pallial region from the flat foot. No shell is formed.

In *Lymnæus*,† as has been already stated, the vitellus undergoes complete division, and the resulting vesicular morula undergoes invagination to produce the hypoblast. Only the middle part of the archenteron becomes the alimentary canal, however. The lateral portions, which take on the form of rounded sacs, may not improbably, as in the Brachiopods, give rise to the perivisceral cavity, though this has not been proved. The mouth is produced by the formation of an opening in the coalesced endoderm and ectoderm, at a point near the anterior end of the body. Upon each side of the mouth a transverse ciliated ridge of the ectoderm is developed, and represents the edge of the velum in other molluscan embryos. Behind this, and on the opposite side of the embryo to that on which the mouth is placed, a raised patch of the ectoderm represents the mantle. The foot commences as a papilla immediately behind the mouth. An involution of the centre of the pallial ectoderm gives rise to a shell-gland, but the proper shell is developed, independently of this, as a cuticular secretion from the whole surface of the mantle.

Thus the embryo of *Lymnæus* possesses an incompletely developed velum, and is, in all essential respects, similar to the veligerous embryo of Lamellibranchs, Pteropods, and Gasteropods; while the Slugs and Land-snails have neither

* 'Entwickelungsgeschichte der *Ampullaria polita*.'

† Lankester, "Observations on the Development of the Pond Snail, *Lymnæus stagnalis*." ('Quarterly Journal of Microscopical Science,' vol. xiv., New Series.)

the velum (unless it be represented by the anterior contractile sac) nor the external embryonic shell.

The development of the *Cephalopoda* is very unlike that of other Mollusks, and will be dealt with under the head of that group.

Fig. 121.

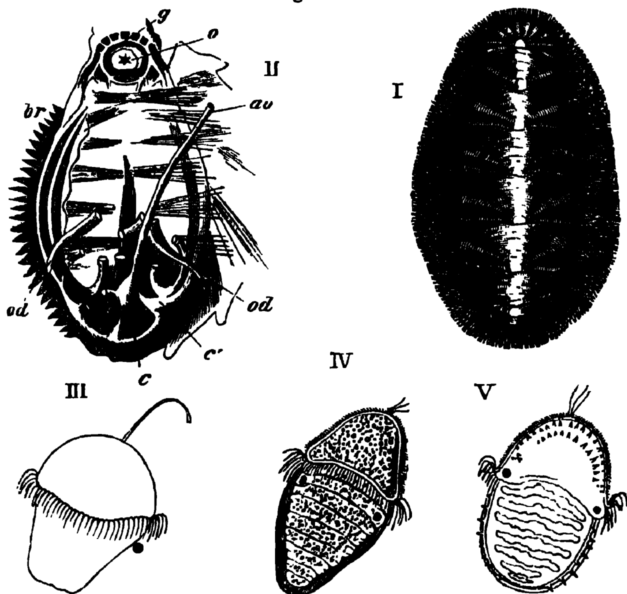


Fig. 121.—I. *Chiton Wossnessenskii.* (After Middendorf.)
II. *Chiton* dissected to show *o*, the mouth; *g*, the nervous ring; *ao*, the aorta; *c*, the ventricle; *c'*, an auricle; *br*, the left branchiæ; *od*, the oviducts. (After Cuvier.)
III. IV. V. Stages of development of *Chiton cinereus*. (After Lovén.)

The lowest forms of the *Odontophora* are the *Polyplacophora*, or *Chitonidæ*, and the *Scaphopoda*, or *Dentalidæ*. The bilateral symmetry of the body is completely or almost completely, undisturbed, while the hæmal wall is flat, or nearly so, and there is no visceral sac.

The POLYPLACOPHORA.—The Chitons (Fig. 121, I.) are elongated, sluglike animals, having the mouth at one end of the body, and the anus at the opposite extremity. A rounded lobe surmounts the mouth, but it bears no eyes nor tentacula, and there is no definite head. The edges of the mantle are thickened, but little prominent, so that the pallial cavity is not much more than an elongated groove, beneath, and internal to, the thickened edge, which is sometimes beset with setæ. In the region in which these setæ occur, the surface of the mantle is covered by a thick cuticula. The setæ, which may be merely chitinous or completely calcified, or partly in the one and partly in the other condition, are developed in sacs lined by the cells of the ectoderm.* In the pallial groove lie the short lamellar processes which represent the branchiæ. The shell is unlike that of any other Mollusk. It consists of eight, transversely elongated, symmetrical pieces, arranged one behind the other, overlapping in such a manner that the posterior edge of the one covers the anterior edge of the next, and articulated together. Sometimes the valves are partially or completely enclosed in the mantle. The heart, composed of a single median ventricle and two lateral auricles, is placed in the middle line, above the rectum, at the posterior end of the body. The aorta is continued forwards from its anterior end, while the auricles receive the blood from the branchiæ. In *Chiton piceus*, according to Schiff,† each auricle communicates by two openings with the ventricle, and the two auricles are united behind. The reproductive organ is median and symmetrical, and its two ducts open on each side of, and not far from, the anus.

The embryo leaves the egg as an oval body, surrounded near its anterior end by a circular ciliated band, behind which an eye-spot appears on each side (Fig. 121, III.). The segments of the shell appear while the young *Chiton* is still locomotive, and the disk in front of the ciliated band

* Reincke, "Beiträge zur Bildungsgeschichte der Stacheln, u. s. w." ('Zeitschrift für Wissenschaftliche Zoologie.')

† 'Zeitschrift für Wissenchaftliche Zoologie,' 1858.

becomes converted into the lobe above the mouth (Fig. 121, IV. V.). The Chitons have existed from the Silurian epoch to the present day, apparently with very little modification.

The SCAPHOPODA.*—In *Dentalium*, the shell is elongated, conical and curved, like an elephant's tusk, with the apex broken off, and it is open at both ends. The animal has a large mantle corresponding in form with the shell, and also open at both ends, the margins of the anterior, larger, aperture being much thickened. The mouth, placed at the extremity of a sort of cup, the margin of which is fringed with papillæ, is situated far behind the anterior opening of the mantle. Behind the oral cup, where the body joins the mantle, is a transverse muscular ridge, from which proceed a great number of long tentacles. These protrude through the anterior opening of the mantle, and play the part of prehensile organs. Behind and below the oral cup the very long subcylindrical foot proceeds. Near its extremity are two lateral fleshy lobes which perhaps correspond with the epipodia of other Mollusks. The oral cup leads into a buccal chamber containing the odontophore, whence the œsophagus passes to the stomach. The liver consists of two symmetrically-branched divisions; and the intestine, after becoming coiled upon itself, ends in a prominent anal papilla, in the median line, behind the root of the foot. There is no heart, but the blood fills spacious sinuses. There are no special respiratory organs distinct from the wall of the pallial cavity. The two renal organs open one on each side of the anus. The renal blood sinus communicates directly with the pallial cavity by two apertures, situated close to those of the renal organs. In the nervous system, the commissures of the parieto-splanchnic ganglia pass directly to the cerebral ganglia, as in the Lamellibranchs. The sexes are distinct and the

* A very complete and accurate account of the organisation of *Dentalium* is given in the monograph of Lacaze-Duthiers, "Histoire de l'organisation, du développement, des mœurs et des rapports zoologiques des Dentales," 1858.

genital gland is single and symmetrical, though its duct opens into the right renal organ. The embryo is at first surrounded by a number of ciliated rings, its anterior end presenting a tuft of long cilia. By degrees, the cilia become restricted to the edges of a disk, into which the anterior end of the embryo expands, and which represents the præ-oral ciliated velum of the Lamellibranchs. The mantle now appears on the dorsal aspect of the body, behind this disk. Its ventral edges are free, and it secretes a shelly plate of corresponding form. But, as development advances, the edges of both mantle and shell unite in the median ventral line, leaving the anterior and the posterior ends open.

The *Scaphopoda* are an ancient group, remains of them occurring as far back as the Devonian Epoch.

The higher *Odontophora* (or the *Gasteropoda*, *Pteropoda*, and *Cephalopoda* of Cuvier) fall into two divisions, according to the structure and arrangement of the parts of the foot. In the one division (the *Gasteropoda* and *Pteropoda*) it may be a simple disk, or it may be divided into three portions—an anterior (the *propodium*), a middle (the *mesopodium*), and a posterior (the *metapodium*); and it may be still further complicated by the development from its sides of muscular expansions—the *epipodia*. But whatever the shape of the foot in these Mollusks, its margins are not produced into prehensile processes, and its antero-lateral portions do not extend beyond the sides of the head, and unite in front of the mouth.

In the other division (the *Cephalopoda*), the margins of the foot are produced into prehensile processes or arms, and the antero-lateral regions of the foot extend over, and unite in front of, the mouth, in such a manner that the latter is placed in the centre of the discoidal foot.*

* See for a valuable discussion of the homologies of the arms and the funnel of the *Cephalopoda*, in which the view here taken is ably, though I do not think, satisfactorily, controverted, Grenacher, "Zur Entwickelungsgeschichte der Cephalopoden." ('Zeitschrift für Wiss. Zoologie,' 1874.)

In the former division, that is in all *Pteropoda*, in all those *Gasteropoda* which breathe the air dissolved in water (*Branchiogasteropoda*), and in some of those which breathe air directly (*Pulmogasteropoda*) the embryo is, as in the *Scaphopoda* and *Polyplacophora*, a veliger; or, at any rate, it has ciliated bands which subserve locomotion. But, in the *Cephalopoda*, no such velum is formed, and the animal acquires the general characters of the adult before leaving the egg.

A shell-gland is often, if not always, present in the embryo of the higher *Odontophora*; and, in all Pteropods and Branchiogasteropods, the mantle secretes a cuticular shell, which, however, may exist only during the larval condition.

If the arrangement of the alimentary canal in a Cephalopod, or a Pteropod, be compared with that which obtains in such a Branchio-gasteropod as *Atlanta*, it will be observed that, in the former, the œsophagus enters the outgrowth of the hæmal region of the body which constitutes the visceral sac, to reach the stomach; and that the intestine passes, at an acute angle with the anterior portion of the alimentary canal, along the posterior face of the visceral sac, to end in the pallial chamber, which is situated on the posterior face of the body. The pedal ganglia consequently lie between lines traversing the anterior and the posterior divisions of the alimentary canal respectively; and hence the alimentary canal has a *neural flexure*, or is bent towards the neural face of the body.

In *Atlanta*, on the other hand, the intestine, when it leaves the stomach, passes along the anterior face of the visceral sac, to reach the pallial cavity, which is situated on the anterior face of the body. Hence lines traversing the two divisions of the alimentary canal would enclose, not the pedal, but the cerebral ganglia. In other words, the intestine is bent in the opposite direction to that which it takes in the Cephalopod, or has a *hæmal flexure*.*

The hæmal flexure of the intestine is very characteristic

* Huxley "On the Morphology of the Cephalous Mollusca." ('Phil. Trans.' 1852.)

of the *Branchiogasteropoda*, and is completed at an early stage of their development.

In such a slightly modified Odontophoran as *Chiton*, the heart presents its normal position in the posterior region of the hæmal face of the body, and has its aortic end turned forwards. Although the branchiæ are situated at the sides of the body, the blood which passes through them must take a backward course to reach the heart; and thus the branchiæ may be said to be virtually behind the heart; and the animal is truly *opisthobranchiate*. It appears to be otherwise with such a Gasteropod as *Buccinum*, in which the gills lie actually in front of the heart; and the animal is therefore said to be *prosobranchiate*. It must be recollected, however, that strictly speaking, no Odontophoran is other than opisthobranchiate. The anus represents the morphological hinder end of the body, and the auricle of the heart, into which the current of blood from the branchiæ passes, is never, morphologically, posterior to the branchiæ.

This is perfectly obvious in the *Cephalopoda*. In the position which the animal frequently assumes and in which it is ordinarily represented, the gills are in front of the heart. But if the Mollusk is placed in its morphologically correct position with the oral face of the arms downwards, it will at once be seen that what is commonly called the ventral face of the animal is the posterior half of its hæmal face, and that the heart lies, morphologically, anterior to the branchiæ.

In such Branchiogasteropods as are prosobranchiate, the gills come to lie in front of the heart in consequence of their having followed the twisted intestine forwards and to the hæmal side of the body.

The PTEROPODA.*—In this group of small pelagic animals there is no distinct head, the eyes and the ordinary tentacles

* See Rang and Souleyet, 'Histoire naturelle des Mollusques Ptéropodes;' and Gegenbaur, 'Untersuchungen über die Pteropoden und Heteropoden,' 1855.

remaining rudimentary. Auditory sacs are attached to the pedal ganglia. Sometimes (*Pneumodermon*) two eversible spinose tentacular organs are developed at the sides of the mouth, and, in addition, two acetabuliferous tentacles take their origin on the inner side of a cup-like hood, which surrounds the anterior end of the body.* *Cymbulia* is stated to possess no radula. The epipodia are large muscular expansions, by the flapping of which the Pteropods swim; but the rest of the foot is always small, and often rudimentary, in correspondence with the small size of the neural face of the body.

The hæmal face, on the contrary, is always produced, as in the *Cephalopoda*, into a relatively large visceral sac; and in some (the *Thecosomata*) this visceral sac is co-extensive with the mantle, which is protected by a shell. In others (*Gymnosomata*) the mantle early disappears, and there is no shell. In *Cymbulia*, the delicate transparent chitinous shell is internal and is invested by an epithelial layer derived from the mantle. In *Spirialis*, the foot bears an operculum. Chromatophores similar to those of the *Cephalopoda* occur in *Tiedemannia*.

In the *Thecosomata*, the free lobe of the mantle, which encloses a spacious pallial cavity, usually lies on the posterior aspect of the visceral sac, as in the *Cephalopoda*, and the rectum terminates in it, on one side of the middle line. In these there is a simple neural flexure of the alimentary canal, as in the Cephalopods, although the turning of the rectum to one side destroys the symmetry of the body. In *Limacina* and *Spirialis*, the intestine appears to be bent round to the anterior face of the visceral sac, the mantle-cavity accompanying it, so that the opening of the mantle is placed on the anterior, instead of on the posterior, face of the visceral sac. There are no distinct gills in the *Thecosomata*, but the lining of the mantle-cavity subserves

* See for the somewhat similar arrangements in *Clione*, Eschricht, 'Anatomische Untersuchungen über *Clione borealis*,' 1858, and Macdonald, "On the Zoological characters of the living *Clio caudata*.' ('Trans. Royal Society of Edinburgh,' 1863.)

the function of respiration, and is sometimes produced into folds, which doubtless aid in the performance of that function. Processes of the body, to which the office of gills is ascribed, are found in some *Gymnosomata* (*Pneumodermon Spongobranchia*).

The heart consists of a single auricle and a single ventricle. The auricle lies close to the pallial cavity, and receives the aerated blood from its walls. The ventricle is sometimes directed forwards (as in all *Gymnosomata*), and sometimes backwards, so that nearly related forms are sometimes opisthobranchiate, sometimes prosobranchiate. The branches of the aortic trunk soon terminate in lacunæ, by which the blood is conveyed back to the walls of the mantle-cavity. The renal organ is a contractile sac with delicate walls, which opens on one side into the pallial chamber, and on the other into the pericardial sinus.

The *Thecosomata* have the principal ganglia concentrated around the gullet—the cerebral ganglia being lateral and united by a long commissure.

In the *Gymnosomata* the ganglia are more scattered, but the arrangement of their nervous system needs re-examination.

All the *Pteropoda* are provided with an *ovotestis*. This is a racemose gland, in the ultimate cæca of which both ova and spermatozoa are developed. The spermatozoa make their appearance at the closed end of the cæcum and accumulate in its cavity; the ova are developed from the epithelial tissue of the cæcum, somewhat lower down; nevertheless fecundation does not take place in the ovotestis, probably in consequence of the ova and spermatozoa attaining maturity at different times. The ovotestis has a single excretory duct, the termination of which may be provided with a *receptaculum seminis* and connected with a penis.

The young of the *Pteropoda* leave the egg provided with a velum, with a rudimentary shell, and probably with an operculum. In most of the *Thecosomata*, the shell is retained and forms the commencement of that of the adult, while the vela disappear and the epipodia are developed.

In *Cymbulia*, the primary external shell is shed and the chitinous internal shell is a secondary development. In the *Gymnosomata*, the primary shell is also cast off, but is not replaced, and three girdles of cilia are developed on the surface of the body.*

The Silurian genera *Tentaculites*, *Theca*, *Pterotheca*, *Conularia*, *Ecculiomphalus* are referred to the *Pteropoda*, but they differ much from all existing forms. Unquestionable *Pteropoda* are not known earlier than the tertiary formations.

The BRANCHIOGASTEROPODA.—In all the members of this group, the development of which has hitherto been studied, the intestine becomes twisted round on to the anterior face of the body, in such a manner that the alimentary canal has a completely hæmal flexure, even in the veligerous embryo. Hence, in the adult, the intestine springs from the hæmal or dorsal, and not from the ventral or neural, aspect of the stomach; and the pallial cavity, when it exists, is placed upon the anterior hæmal face of the body.

In the embryo, the shell always makes its appearance as a conical, symmetrical, median cap. This embryonic shell usually persists at the apex of that of the adult, the form of which is modelled upon that of the visceral sac, and hence, like the latter, is usually spiral. The embryo is also very generally, if not universally, provided with an operculum.

The shell and operculum of the embryo disappear in the naked Branchiogasteropods; but the primitive external shell is sometimes replaced by an internal shell lodged in a cavity of the mantle (*e.g. Aplysia*). Usually, the Branchiogasteropods possess a distinct head provided with a pair of tentacles and with two eyes, which may either be sessile or mounted upon peduncles of their own.

* Gegenbaur, *l. c.*; Krohn, "Beitrage zur Entwickelungsgeschichte der Pteropoden und Heteropoden," 1860; and Fol, "Etudes." ('Archives de Zool. Expérimentale,' 1875 and 1876.)

The mouth may be armed with chitinous jaw-plates, in addition to the radula. The heart is generally composed of a ventricle and a single auricle, but sometimes there are two auricles.

The *Branchiogasteropoda* fall into two distinct series, of which the one is hermaphrodite (the genital gland being an ovotestis) and invariably opisthobranchiate; while the other is unisexual and usually prosobranchiate. In each series, there are some forms which are provided with a large mantle; and others, in which the mantle is altogether abortive (*Nudibranchiata, Firola*). These *chlamydate* and *achlamydate* Branchiogasteropods correspond with the *Thecosomata* and *Gymnosomata* among the Pteropods.

The chlamydate Branchiogasteropods are usually provided with branchiæ, which either take the form of numerous lamellæ, or of two plume-like organs, sometimes reduced to one functional gill and a rudiment of the second. In the achlamydate forms, true gills are usually absent, though they may be replaced functionally by processes of the hæmal body-wall.

Among the *Opisthobranchiata, Phyllidia* is nearly symmetrical, the anus being situated at the posterior end of the body, and there is a large mantle, devoid of a shell. There is no pallial cavity, and the branchiæ are numerous lamellæ, placed on each side of the body, between the free edge of the mantle and the foot. In *Aplysia*, the mantle is relatively small, and possesses an internal shell; the branchiæ, the anus, and the reproductive apertures are placed on the right side of the body. In this genus, and in *Gasteropteron*, there are very large epipodial lobes, by the aid of which some species propel themselves like Pteropods.

The *Nudibranchiata* have no mantle, and the anus is usually situated on the right side of the body; sometimes, however, as in *Doris*, it is terminal. In the pelagic *Phyllirhöe*, the foot aborts, as well as the mantle, and the body has the form of an elongated sac.

The gastric portion of the alimentary canal becomes

complicated by division into several portions, some of which are provided with chitinous or calcareous plates, or teeth, in *Aplysia*, *Bulla*, and other genera. In many Nudibranchs, as *Eolis*, the liver is represented by a much-branched tubular organ, the cæcal ultimate ramifications of which end in the elongated dorsal papillæ. The apices of these papillæ contain thread cells.

In the series of the *Prosobranchiata*, the great majority are not only chlamydate, but there is a spacious branchial chamber, and the pallial wall of the body is produced into a conical visceral sac, which contains the stomach, liver, and genital organs. It is usually asymmetrically coiled, and is protected by the shell. No Opisthobranch possesses a large visceral sac of this kind. On the other hand, no Prosobranch is, like *Phyllidia*, symmetrical, with the anus at the posterior end of the body. *Patella* and *Fissurella* are nearly symmetrical, but the anus is anterior.

The *Prosobranchiata* have, at most, rudiments of *epipodia*, but the rest of the foot often acquires a much greater development than in the *Opisthobranchiata*, and a chitinous or shelly plate—the operculum—is frequently developed from the dorsal or hæmal aspect of the metapodium. The differentiation of the foot attains its highest degree in the so-called *Heteropoda*, in which the propodium, mesopodium, and metapodium differ widely in form,—the propodium being broad and fin-like, and constituting the chief organ of locomotion in these free-swimming oceanic animals.

In the Limpets (*Patellidæ*), the visceral sac forms merely a conical projection of the hæmal surface, and the numerous lamellar, or filamentous, respiratory organs, are lodged between the free edges of the mantle and the sides of the body. In the other chlamydate *Prosobranchiata*, except the *Cyclostomata*, there are two plumose gills lodged in a pallial chamber situated on the anterior face of the visceral mass, which is usually large and spirally coiled. Sometimes, as

in the division of the *Aspidobranchia*, the two branchiæ are equal or nearly equal in size. Sometimes one is so much smaller than the other as to be nearly abortive (*Ctenobranchia*). *Ampullaria* has a pulmonary cavity as well as gills. On the other hand, the *Cyclostomata* have no branchiæ, but breathe air by means of the parietes of the pallial chamber, whence they are ordinarily reckoned among the *Pulmonata*, which they resemble in their terrestrial habits. In many *Prosobranchiata*, the wall of the branchial chamber is produced into a muscular spout-like prolongation, termed the *siphon*, which serves to direct the branchial current. The presence of this siphon is usually accompanied by a notch or grooved process of the shell, and by carnivorous habits.

In the *Heteropoda*, there is a gradual reduction of the mantle, from *Atlanta*, in which the mantle and shell have the ordinary proportions, and the departure from the ordinary Gasteropod type is but little greater than that observed in *Strombus* and *Pteroceras*, through *Carinaria*, in which the mantle is much reduced, and the shell is a mere conical cap, to *Firola*, in which the mantle and shell are wanting in the adult, and which, therefore, correspond with the achlamydate *Pteropoda* and *Opisthobranchiata*.

In many genera of the *Ctenobranchia*, and especially among the carnivorous forms, the mouth is situated at the end of a long proboscis, which contains the odontophore, and a great part of the long œsophagus. This proboscis is protruded and retracted by special muscles.*

The eggs are often laid in capsules secreted by the walls of the oviduct. In *Neritina*, *Purpura*, and *Buccinum*, each capsule contains a considerable number of ova, but of these only a few (one in *Neritina*) become embryos, and devour the rest.†

* See the description of the proboscis of the Whelk in Cuvier's 'Mémoires sur les Mollusques.'

† Koren and Daniellssen, "Recherches sur le développement des Pectinibranches" ('Fauna littoralis Norvegiæ,' ii. 1856), and Carpenter "On the development of the embryo of *Purpura lapillus*" (Trans. Micr. Society, 1854, and 'Annals of Nat. Hist.,' 1857). Claparède, "Anatomie und

The parasitic habit which is so rare among the *Mollusca* occurs in the genus *Stylifer*, which infests Star-fishes and Sea-urchins, sometimes imbedding itself in the perisoma; and, under a very remarkable and not yet thoroughly understood form, in the singular parasite of another Echinoderm, *Synapta digitata*, termed by its discoverer, Müller, *Entoconcha mirabilis*.*

In some few of the *Synaptæ* (not more than one, or perhaps two, in a hundred), elongated tubular *molluskigerous sacs* are found attached by one extremity to one of the intestinal vessels; while the opposite end either hangs freely into the perivisceral cavity, or may be entangled among the bases of the tentacles, at the cephalic extremity of the body of the *Synapta*. The sac is closed, but, at its attached end, a long invagination extends into its interior. The cavity of the sac beyond the closed extremity of the invagination contains an ovary; and, beyond this, a certain number of free seminal capsules. The ova are detached from the ovary, and undergo their development in envelopes, each containing many ova, which gradually fill the cavity of the molluskigerous sac. From these ova, embryos, provided with a velum, shell, and operculum proceed. A large pallial cavity is soon apparent; but, in the most advanced stages of development observed, it contained no branchiæ.

What becomes of these larvæ is unknown, nor is it even certain to what group of the *Odontophora*, *Entoconcha* belongs.

The PULMONATA.—These are odontophorous Mollusks which breathe air directly, by means of a respiratory surface furnished by the wall of the pallial cavity.

In some, such as the *Peroniadæ* (Fig. 123) and *Veronicellidæ*, the body of the slug-like animal is very nearly

Entwickelungsgeschichte der *Neritina fluviatilis*." ('Archiv für Anatomie,' 1857.)

* 'Die Erzeugung von Schnecken in Holothurien,' 1852. Baur, "Ueber *Synapta digitata*." ('Nova Acta,' xxxi. 1864.)

symmetrical; the anus and the lung-sac being situated close together at the posterior extremity of the body. The mantle is large, and extends over the whole hæmal or dorsal surface. In all the other *Pulmonata*, the pulmonary and the anal apertures lie on the right side of the body, and the mantle is provided with at least the rudiments of a shell. The pallial region is sometimes very small in proportion to the rest of the body, and then forms a flattened disk, as in the common Slug; while, in some *Limacidæ* and *Testacellidæ*, and in the *Janellidæ*, the mantle is so much reduced that they are almost achlamydate. In the Snails, the mantle is large and is produced into an asymmetrically coiled visceral sac, in which the stomach, liver, and genital gland lie. The mantle-cavity lies on the fore part of the sac, and the anus opens on its margin. Thus, in all the ordinary *Pulmonata*, the termination of the intestine is twisted from its normal position at the hinder end, forwards to the right dorsal, or hæmal, aspect of the body.

When the pulmonary sac is posterior, and the pallial region small, the ventricle of the heart is anterior, and the auricle posterior, and the animal may be said to be *opisthopulmonate*. On the other hand, when the pallial region is large, and gives rise to a visceral sac, with the concomitant forward position of the pulmonary chamber, the auricle is inclined more or less forwards and to the right side, and the apex of the ventricle backwards and to the left side. The animal is thus more or less *prosopulmonate*.

The mouth is commonly provided with a horny upper jaw, as well as with a well-developed odontophore. Large salivary glands are usually present.

The heart consists of a single auricle and a single ventricle. The aortic trunk, which proceeds from the apex of the latter, divides into many branches, but the venous channels are altogether lacunar. A renal organ lies close to the pulmonary sac in the course of the current of the returning blood.

There are usually two simple eyes, often lodged in the summits of retractile tentacula.

The *Pulmonata* are hermaphrodite. The generative gland

Fig. 122.

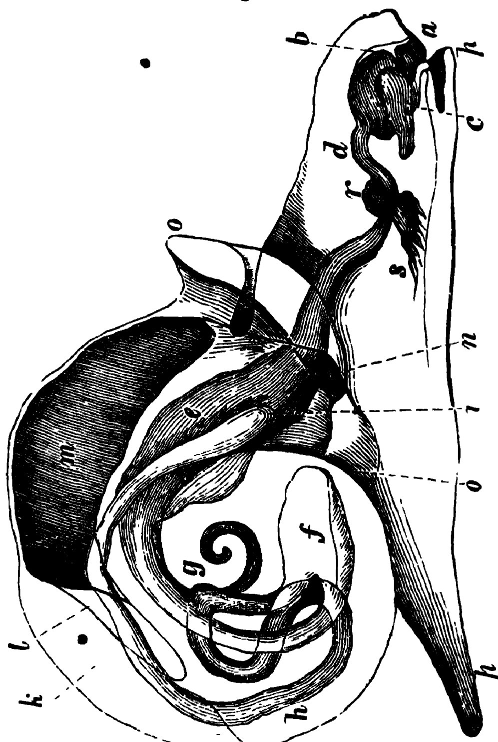


Fig. 122.—Diagram exhibiting the disposition of the intestine, nervous system, etc., in a common Snail (*Helix*).—*a*, mouth; *b*, tooth; *c*, odontophore; *d*, gullet; *e*, its dilatation into a sort of crop; *f*, stomach; *g*, coiled termination of the visceral mass: the latter is also close to the commencement of the intestine, which will be seen to lie on the neural side of the œsophagus; *h*, rectum; *i*, anus; *k*, renal sac; *l*, heart; *m*, lung, or modified pallial chamber; *n*, its external aperture; *o*, thick edge of the mantle united with the sides of the body; *p*, foot; *r*, *s*, cerebral, pedal, and parieto-splanchnic ganglia aggregated round the gullet.

is an ovotestis, and is composed of branched tubuli, from

the cellular contents of which both ova and spermatozoa are developed (Fig. 123, III.).

A narrow common duct leads from the ovotestis, and, soon dilating, receives the viscid secretion of a large albumen gland. The much wider portion of the common duct beyond the attachment of this gland is incompletely divided by longitudinal infoldings into a sacculated, wider, and a straight, narrower, division. The former conveys the ova, and the latter the spermatozoa. At the end of this part of the apparatus, the wider portion, which represents the oviduct, passes into the vagina, which opens at the female genital aperture, while the narrower portion of the common duct is continued into a separate, narrow, vas deferens, the end of which opens into a long invagination of the integument—the penis. In *Peronia*, the vas deferens and the oviduct open together by the genital aperture, and, as in some Branchiogasteropods, a groove, along which the seminal fluid is conducted, leads to the outer opening of the eversible penis (Fig. 123, I. II.).

In connexion with the female genital aperture, there is always a *spermatheca*, or sac (which is sessile in the Slugs, but in the Snails is placed at the extremity of a long duct) for the reception of the semen of the other individual when copulation takes place.

The *Helicidæ* alone possess, in addition, the so-called *sac of the dart*, a short muscular bag, in which pointed chitinous or calcified bodies—the *spicula amoris*—are formed; and certain glandular cæca, generally arranged in two digitate bundles, termed *mucous glands*, which give rise to a milky secretion. Sometimes, *prostatic glands* are developed on the vas deferens, which may be dilated in part of its course into a *vesicula seminalis*.

The ova are impregnated high up in the oviduct, and are invested by a relatively very large mass of albumen and enclosed within a thick, sometimes calcified chorion. The mass enclosed by the latter may be a tenth of an inch or more in diameter, while the proper ovum may have not more than a twelfth of that size.

There is no trustworthy evidence of the existence of the opisthobranchiate Gasteropods before the epoch of the Trias, but it is to be remembered that the great majority of these animals have no shells. Of the rest of the preceding groups of *Odontophora*, representatives are known as far back as the middle of the Palæozoic epoch, while *Pteropoda, Hetero-*

Fig. 123.

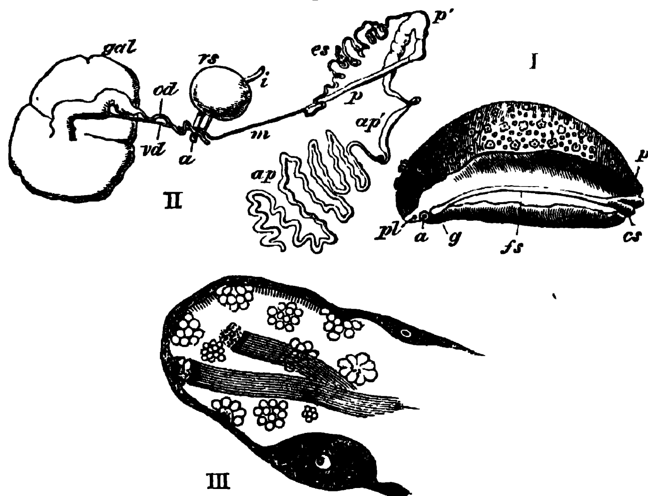


Fig. 123.—I. *Peronia verruculata.*—*a*, anus; *pl*, pulmonary aperture; *g*, genital aperture; *fs*, seminal groove; *p*, opening for the penis.
II. Generative organs of the same animal, the ovotestis being omitted. *gal*, gland which furnishes a glairy secretion; *od*, oviduct; *vd*, vas deferens; *i*, intestine; *a*, anus; *rs*, receptaculum seminis, *p*, aperture of the penis; *p'*, penis; *cs*, seminal duct; *ap*, glandular appendage; *m*, retractor muscle of the penis. (After Keferstein.)
III. Blind end of a follicle of the ovotestis of *Helix pomatia*. At the apex the spermatozoa are seen in different stages of development, the fully formed spermatozoa floating in bundles in the cavity of the follicle. Lower down, ova are developing in the walls of the follicle. (After Keferstein and Ehlers.)

poda, and *Prosobranchiata* occur in the Silurian formations. Among the *Prosobranchiata*, the *Patellidæ* and the *Aspidobranchia* are the characteristic forms of the older formations,

the *Ctenobranchia* appearing later, and acquiring their present relative abundance only in the later secondary, and the tertiary epochs.

The CEPHALOPODA.—The bilateral symmetry which is so obvious in the *Polyplacophora* and the *Scaphopoda* is but

Fig. 124.

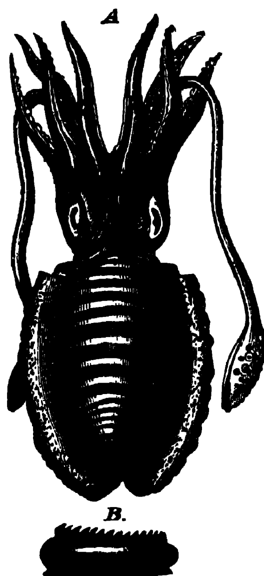


Fig. 124.—A, *Sepia officinalis*. B, Lateral view of the horny ring of an acetabulum.

little disturbed in this group of the *Odontophora*. The mouth and the anus are situated in the median plane, which divides the body into corresponding halves; while the branchiæ, two or four in number, are disposed symmetrically on each side of this plane, as are the brachial prolongations of the margins of the foot. The hæmal face of the body,

however, is not flat, as in the mollusks which have just been mentioned, but is elongated perpendicularly to the neural face, so as to form a sort of sac, invested by the mantle. On the posterior, or anal, face of the sac, the mantle enclose a large pallial cavity, in which the branchiæ are protected. On the anterior aspect of the sac, on the contrary the mantle may have no free edge, or, at most, forms a comparatively small flap.*

The integument is provided with *chromatophores*, which are sacs with elastic walls, full of pigment, and provided with radiating muscles, by which they may be drawn out to a size many times greater than that which they possess in their contracted state. In their dilated condition, the colour proper to the contained pigment becomes plainly visible, while in their contracted state they appear as mere dark specks. It is to the successive expansion and contraction of these chromatophores that the Cephalopoda owe the peculiar play of "shot" colours, which pass like blushes over their surface in the living state. These blushes of colour are especially well displayed by young Cephalopods just freed from the egg.

But that which particularly distinguishes the Cephalopods, is the form and disposition of the foot. The margins of this organ are, in fact, produced into eight or more processes termed arms, or *brachia;* and its antero-lateral portions have grown over and united in front of the mouth, which thus comes, apparently, to be placed in the centre of the pedal disk. Moreover, two muscular lobes which correspond with the epipodia of the Pteropods and Branchiogasteropods, developed from the sides of the foot, unite posteriorly, and, folding over, give rise to a more or less completely tubular organ—the funnel, or *infundibulum.* The open end of the funnel projects between the posterior face of the body and the pallial wall of the branchial cavity, and serves to conduct the water, when it is driven

* Cephalopods are usually described as if the oral end of the body were the upper end, and the face on which the pallial chamber is placed ventral—a method which seriously interferes with the comprehension of their relations with other Mollusks.

out of the latter by the contraction of the mantle in

Fig. 125.

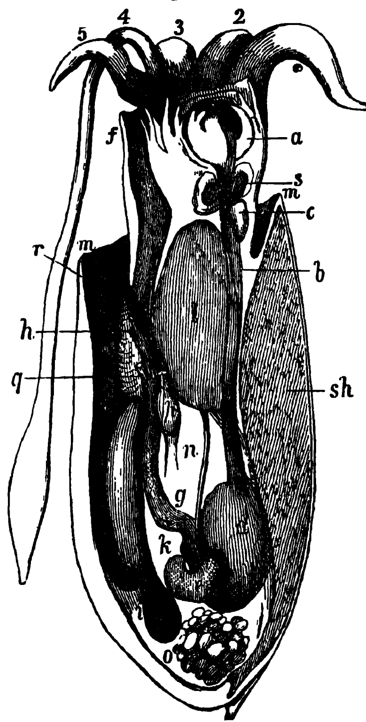


Fig. 125.—Diagrammatic section of a female *Sepia*.—*a*, Buccal mass surrounded by the lips, and showing the horny jaws and tongue; *b*, œsophagus; *c*, salivary gland; *d*, stomach; *e*, pyloric cæcum; *g*, the intestine; *h*, the anus; *i*, the ink-bag; *k*, the place of the systemic heart; *l*, the liver; *n*, the hepatic duct of the left side; *o*, the ovary; *p*, the oviduct; *q*, one of the apertures by which the water-chambers are placed in communication with the exterior; *r*, one of the branchiæ; *s*, the principal ganglia aggregated round the œsophagus; *f*, the funnel; *m*, the mantle; *sh*, the internal shell, or cuttle-bone. 1, 2, 3, 4, 5, the produced and modified margins of the foot, constituting the so-called arms of the *Sepia*.

ordinary expiration; and when the animal swims, the stream

forcibly driven out in this way causes it to dart swiftly backwards.

The aperture of the mouth (Fig. 125, *a*) is provided with a hard chitinous beak, like that of a parrot, the two divisions of which are anterior and posterior. Of these, the anterior is always the shorter, and is overlapped by the other.

Within the cavity of the mouth is an odontophore, with its radula (Fig. 126, II.); and the long gullet passes back on the middle line to open into the stomach, which is situated towards the middle, or the end, of the mantle-sac. From the stomach, the intestine, more or less bent upon itself, passes towards the neural aspect of the body, and ends in the median anus. Hence the alimentary canal has a well-marked neural flexure (Fig. 125).

Except in *Nautilus*, one or two pairs of salivary glands are present (Fig. 126, I. *s'*). The liver (Fig. 126, I. *h*) is always large; and there are two hepatic ducts (Fig. 126, I. *dh*), beset for a greater or less extent with glandular follicles, generally considered to be pancreatic in function. Very often a large, sometimes spirally wound, cæcum is developed from the commencement of the intestine; into this the hepatic ducts open.

The heart (Fig. 127, *c*) is placed upon the posterior face of the body on the hæmal side of the intestine, and receives the blood by branchio-cardiac vessels, which correspond in number with the gills; and, as they are contractile, might be regarded as auricles. The gills themselves have no cilia, and are, in some cases, if not always, contractile. The arteries end in an extensively developed capillary system, but the venous channels retain to a greater or less extent the character of sinuses.* The venous blood, on its way back to the heart, is gathered into a large longitudinal sinus—the *vena cava*—which lies on the posterior face of the body, close to the anterior wall of the branchial chamber, and divides into as many afferent

* Milne-Edwards, 'Recherches Anatomiques et Zoologiques. Première partie.' 'Observations et expériences sur la Circulation chez les Mollusques,' 1845.

branchial vessels as there are gills. Each of these vessels traverses a chamber which communicates directly with the mantle-cavity, and the wall of the vessel which comes into contact with the water in this chamber is sacculated and glandular * (Fig. 127, *re*). Each chamber, in fact, represents a renal organ. The pericardium, and the sacs in which the testes and ovaria are lodged, may communicate with the pallial cavity either directly or through these chambers. Thus in *Sepia officinalis*, Krohn † observed that the renal chambers communicate not only with the cavities in which the branchial hearts are lodged, but with a chamber which contains the stomach and the spiral pyloric appendages; and that all these cavities are distended when air is blown into one renal chamber. In *Eledone*, on the contrary, he found, and I have repeated the observation, that one renal chamber can be fully distended without the air passing into the other.

In *Nautilus pompilius*, there are, as Valenciennes discovered, three pairs of openings, which lead from the branchial sac into chambers contained in the interior of the body. Of these chambers there are five; the anterior and posterior pairs are situated on each side of the rectum, and each has its own opening; the fifth, a very much larger

* On account of the transparency of the tissues in the living *Loligo media*, this species affords an easy opportunity of observing the rhythmical contractions of the branchiæ and their afferent and efferent vessels. For this purpose the mantle should be laid open, and the nidimental glands carefully removed. The sacculated afferent veins and the branchial hearts contract about sixty times a minute. The pulsations of these veins and of the branchial hearts are not synchronous. The branchial veins and the lamellæ of the branchiæ also contract rhythmically, but I could observe no contraction in the branchial arteries. The portion of the branchial vein which lies between the base of the gill and the systemic ventricle is very short, and it is hard to say whether it contracts independently or not. Mechanical irritation causes contraction both of the afferent branchial veins and of the branchial hearts.

In the living *Eledone cirrhosus*, I have observed regular rhythmical contractions of the vena cava itself as well as of its divisions, the sacculated afferent branchial veins, of the branchial hearts and of the branchiocardiac vessels.

† "Ueber die wasserführende System einiger Cephalopoden." ('Archiv für Anatomie,' 1839.)

chamber, has two openings, one on each side. It is co-extensive with that part of the mantle which lies behind

Fig. 126.

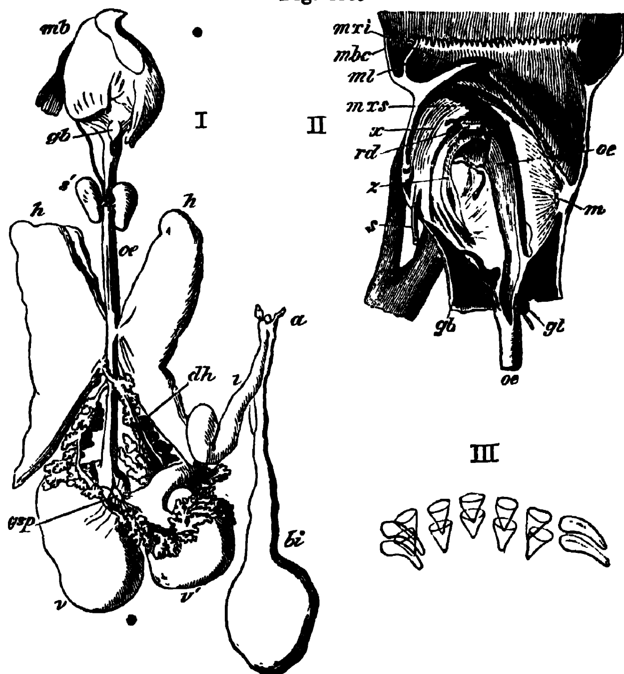


Fig. 126.—*Sepia officinalis*.—I. The alimentary canal with the ink bag; *mb*, buccal mass; *gb*, inferior buccal ganglion; *s'*, posterior salivary glands; *œ*, œsophagus; *h*, liver; *dh*, hepatic duct; *v*, stomach; *v'*, pyloric cæcum; *i*, intestine; *a*, anus; *bi*, ink bag; *gsp*, splanchnic ganglion on the stomach. (After Keferstein.)
II. Longitudinal and vertical section through the buccal mass; *mxi*, posterior beak; *mxs*, anterior beak; *mbc*, buccal membrane; *ml*, lip; *x*, gustatory (?) organ; *rd*, radula; *z*, sac of the radula; *s'*, salivary gland; *gl*, superior buccal ganglia. (After Keferstein.)
III. A single transverse row of teeth from the radula (after Troschel).

the insertion of the shell muscles and the horny band which connects them. It is separated from the paired chambers

by their inner walls, and these walls are traversed by the afferent branchial veins. Appendages of these veins project on the one hand into the paired chambers, and on the other into the single chamber. The latter appendages are elongated papillæ, while the former are lamellar. Earthy concretions, composed mainly of phosphate of lime, but which yield no trace of uric acid, are usually found in the paired sacs.*

Fig. 127.

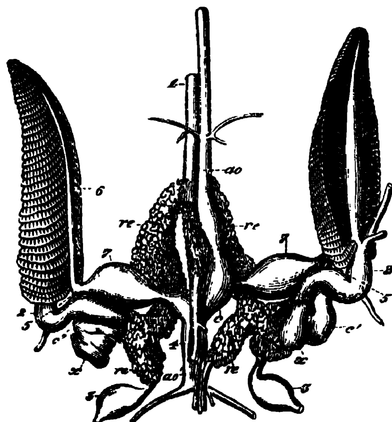


Fig. 127.—*Sepia officinalis.*—*c*, systemic heart; *ao*, anterior aorta, *ao'*, posterior aorta; 1, vena cava; 2, afferent branchial vessels; *re*, renal organs; *z*, appendages of these vessels; 3, 4, large posterior veins bringing blood to the afferent branchial vessels; 5, 6, 7, efferent branchial vessels, branchial veins, and branchio-cardiac or auricular trunks. (After Hunter.)

The nervous system in the *Cephalopoda*, as in other *Mollusca*, consists of cerebral, pedal, and parieto-splanchnic ganglia, aggregated around the gullet, and connected by

* Owen, 'Memoir on the Pearly Nautilus.' Van der Hoeven, "Beitrag zur Anatomie vom *Nautilus pompilius*" ('Archiv für Naturgeschichte,' 1857). Huxley, "On some points in the anatomy of *Nautilus pompilius*" (Proceedings of the Linnean Society, 1858) See also Keferstein, Bronn's 'Klassen u. Ordnungen,' Bd. iii. (1862–66), pp. 1390, 1319.

commissural cords. In addition to these, buccal, visceral, branchial, and pallial ganglia may be developed on the nerves which supply the buccal mass, the alimentary canal, heart, branchiæ, and mantle.

In the *Dibranchiata* (Fig. 128), the three principal pairs of ganglia are usually large, and so closely aggregated together that the commissures are not readily distinguishable. The optic nerves are very large; one or two nerves are given off to the superior or anterior buccal ganglia, which have coalesced into one mass, and are united by commissures, which encircle the œsophagus, with the coalesced inferior or posterior buccal ganglia. The pedal ganglia lie on the posterior side of the gullet, and supply the large nerves to the arms, and those to the funnel, while the auditory nerves are immediately connected with them. Each parieto-splanchnic ganglion gives off a nerve which runs along the shell-muscles to the anterior wall of the mantle, and there enters a large ganglion, the *ganglion stellatum*. A large median branch, or branches, from the parieto-splanchnic ganglia, accompanies the vena cava, and is distributed to the branchiæ and sexual organs. The inferior buccal ganglion sends a recurrent nerve along the œsophagus, which ends in a ganglion on the stomach.*

The nervous system of *Nautilus* differs in some important particulars from that of the *Dibranchiata*. The cerebral ganglia are represented by a thick transverse cord, which lies in front of the œsophagus, and from the outer angles of which the optic and olfactory nerves are given off, while nerves to the buccal mass proceed from its anterior edge. The pedal ganglia lie close to the cerebral ganglia, and are united by a slender commissure, which passes behind the gullet. They supply all the brachial processes and the funnel with nerves, and the short auditory nerves are connected with them. The parieto-splanchnic ganglia are, like the cerebral ganglia, elongated, and together constitute a thick cord, which, united at each end with the cerebral gan-

* See Hancock, "Anatomy of the nervous system of *Ommastrephes*." ('Ann. Nat. History,' 1852.)

glia, forms a hoop round the gullet, distinct from the pedal nerve-arch, and separated from it by a process of the cartilaginous skeleton. The largest nerves given off from these ganglia are those which go to the branchiæ.

Eyes, olfactory organs, and auditory sacs are always present. The eyes of the *Cephalopoda* may be lodged in orbital cavities at the sides of the head, as in all the *Dibranchiata*; or may be pedunculated, as in *Nautilus*. In the former case, the eye is enclosed partly by the cephalic cartilage, to

Fig. 128.

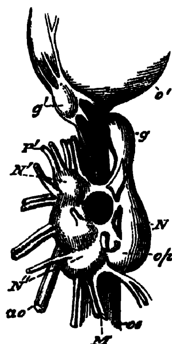


Fig. 128.–
gullet;
ganglion; [illegible]
nerves to the anus; M, pallial nerves; *g*, superior; *g'*, inferior buccal ganglion. (After Garner.)*

which sometimes special orbital cartilages are added, and partly by a fibrous capsule continuous with these. The fibrous capsule becomes transparent over the eye, and gives rise to what is variously interpreted as the representative of the cornea, or as that of the eyelids of vertebrated animals. This transparent coat is sometimes entire, or presents only a small perforation (*Octopus*, *Sepia*, *Loligo*, and the other *Myopsidæ* of D'Orbigny); sometimes it has a

* Trans. Linnean Society, 1836.

wide opening, through which the crystalline lens may project (*Loligophes*, *Ommastrepsis* and the other *Oigopsidæ* of D'Orbigny); and sometimes it is altogether absent, and the capsule of the eye becomes an open cup (*Nautilus*).

In the *Dibranchiata*,* a great part of the chamber of the capsule of the eye is occupied by the ganglion, into which the optic nerve enlarges after entering it; by muscles; and by a peculiar white glandular substance. Lining the capsule, but not adhering to its inner surface, in front, is the silvery *tapetum*, formed of two layers. These pass into one another at the edges of the free prolongation of the tapetum, which forms the iris. Longitudinal muscular fibres are interposed between the two layers of the tapetum. Under the tapetum is a layer of cartilage, which forms the *inner capsule* of the eye, extends as far as the iris externally, and is perforated by the fibres of the optic nerve on its inner side. The free edge of the inner capsule gives attachment to a thick rim of connective tissue, containing muscular fibres. This so-called *ciliary body* enters the deep groove which surrounds the lens; the latter is, in fact, made up of layers of structureless membrane, which are cuticular productions of the ciliary body. In shape, the lens is elongated in the direction of the axis of the eye, so as to be almost a cylinder with convex ends, and thus, with its deep equatorial groove, into which the ciliary body fits, it has a wonderful resemblance to a Coddington lens. The vitreous humour is a transparent fluid. The retina lines the inner capsule, and may be divided into an outer and an inner stratum, separated by a pigment layer. The inner stratum is formed of prismatic or cylindrical rods, the outer ends of which abut upon the pigment, while their inner ends, turned towards the cavity of the eye, are covered by a thick hyaloid membrane. The outer stratum contains the plexus of the fibres of the optic nerves, and numerous cells (ganglionic), supported by connective tissue. The terminations of the nerves therefore must traverse the pigment layer to reach the rods.

* See Hensen, "Ueber das Auge einiger Cephalopoden." ('Zeitschrift für Wissenschaftliche Zoologie,' 1865.)

It will be observed that the apparent resemblances between the cephalopodous and the vertebrate eye are merely superficial, and disappear on detailed comparison.

In *Nautilus*, the eye has neither cornea, lens, nor vitreous humour, but is a mere cup, lined by the retina. The aperture for the admission of light is exceedingly small.

The olfactory organs, the true nature of which was discovered by Kölliker,* are sometimes pits, sometimes papillæ of the integument, situated behind or above the eyes. In the *Teuthidæ* and *Sepiadæ* they are depressions above the eyes; in the *Octopoda*, they are either depressions or papillæ (*Argonauta* and *Tremoctopus*) in the same position, but nearer the anterior face of the body. In *Nautilus*, they are elongated, tentaculiform, and situated immediately behind the eyes.

In the *Dibranchiata*, the auditory sacs are lodged in cavities of the cephalic cartilage, and contain a single large otolith, composed of carbonate of lime, and of rounded or irregular, but definite and characteristic form. In *Nautilus*, Dr. Macdonald discovered that the auditory sacs are attached to the pedal ganglia, and are not lodged in the cranial cartilage. They contain numerous otoliths.

An endoskeleton formed of true cartilage is developed in the region of the principal ganglia, and sometimes furnishes them with a complete investment. It gives attachment to the most important muscles. In some Cephalopods additional cartilages appear in the mantle and in the funnel. The muscular fibres of the *Cephalopoda* are unstriated.

The sexes are distinct, and the reproductive organs are unlike those of other Mollusks. They consist, in both sexes, (Fig. 129) of lamellar or branched organs, the cellular contents of which are metamorphosed into ova or spermatozoa, and which are attached to one point or line of the wall of a chamber, which communicates with the pallial cavity by two symmetrically disposed oviducts, in the females of some species; but, in most female and almost all male, Cephalo-

* 'Entwickelungsgeschichte der Cephalopoden,' 1841, p. 107.

pods* it has only one duct, the termination of which is usually situated on the left side, but may be near the middle line (male *Nautilus*), or even on the right side (female *Nautilus*). In the female, the oviduct, or oviducts, present glandular enlargements. In addition, two lamellar *nidamental glands* are developed upon the walls of the branchial cavity, and to these accessory glands may be added. These

Fig. 129.

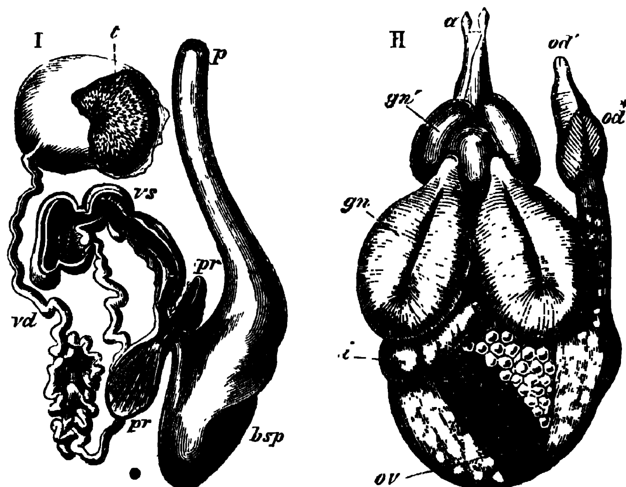


Fig. 129.—*Sepia officinalis.*—I. male organs, *t*, testis; *vd*, vas deferens; *vs*, vesicula seminalis; *pr*, prostate; *bsp*, receptacle of the spermatophores; *p*, penis with the genital aperture (After Duvernoy.)
II. Female genital organs.—*a*, anus; *i*, intestine; *ov*, ovary; *od'*, oviducal aperture; *od*, oviducal gland; *gn*, nidamental gland; *gn'*, accessory glands. (After Milne-Edwards.)

glands secrete a viscid fluid, which invests the ova, and connects them, when laid, into variously shaped aggregations. In the male, a prostatic gland furnishes the material of the cases, or *spermatophores,* in which packets of sperma-

* Keferstein found two ducts in a male *Eledone moschata.*

tozoa are contained, and which sometimes possess a very complicated structure.

In the *Dibranchiata*, the spermatophores are slender cylindrical bodies which may reach half an inch in length. They have an external structureless case, thinner at one end than the other, and often ending in a fine filament at the thin end. Within this case, filling its thicker end, and as much as half or two-thirds of the rest of its cavity, is a delicate sac full of spermatozoa.

The rest of the case is occupied by a very singular elastic body, in form somewhat resembling the sponge of a gun with a spiral screw turned on the handle. The enlarged 'sponge' end of this body is fastened by a delicate prolongation to the spermatic sac, while the 'handle,' being too long to lie straight, is coiled up at the end opposite to the sponge and then fastened to the outer case. When these bodies come into contact with water they undergo strange contortions, and finally, the thin end of the case giving way, the spring frees itself, starts out of the case and drags with it the spermatic sac.*

In *Nautilus*, according to Van der Hoeven, the spermatophores have a much simpler structure.

The male Cephalopods are distinguished from the females by the asymmetry of their arms, one or more of which, on one side, are peculiarly modified, or *hectocotylised*.

Some Cephalopods are devoid of any shell, but most possess a pallial shell, which is either external or internal. In the former case, the visceral sac is lodged within that part of the cavity of the shell which lies nearest its open end, and the rest of the cavity is divided into chambers, which contain air, by transverse *septa*. The septa are perforated, and a prolongation of the mantle—the *siphuncle*—is continued through the series of perforations, as far as the apical chamber of the shell. The internal shells of the

* For the minute structure of these curious spermatic cartridges, see Milne-Edwards' elaborate essay, "Observations sur les Spermatophores des Mollusques Céphalopodes" ('Annales des Sciences Naturelles,' 1840).

Cephalopods may have very various forms, and may even be chambered and siphunculated; but, in this case, the chamber nearest the mouth of the shell is small, and incapable of lodging the viscera.

Our knowledge of the development of the Cephalopods is confined to that of the *Dibranchiata*.* In these, the yelk undergoes partial division, and the blastoderm, formed upon one face of it by the smaller blastomeres, spreads gradually over the whole ovum, enclosing the larger and more slowly dividing blastomeres. The mantle makes its appearance as an elevated patch in the centre of the blastoderm, while the future arms appear as symmetrically disposed elevations of the periphery, on each side of the mantle. Between these and the edge of the mantle, two longitudinal ridges mark the rudiments of the epipodia, while the mouth appears in the middle line in front of the mantle, and the anus, with the rudiments of the gills, behind it. The rest of the blastoderm forms the walls of a vitelline sac, enclosing the larger blastomeres.

The pallial surface now gradually becomes more and more convex, the posterior margin of the mantle growing into a free fold, which encloses the pallial chamber and covers over the gills.

The internal shell is developed in a sac formed by an involution of the ectoderm of the mantle. The epipodia unite behind, and give rise to the funnel, while the antero-lateral portions of the foot grow over the mouth, and thus gradually force the latter to take up a position in the centre of the neural face, instead of in front of it. The yelk-sac gradually diminishes, and the contained blastomeres are finally taken into the interior of the visceral sac, into which the alimentary canal is gradually drawn.

* Kölliker, 'Entwickelungsgeschichte der Cephalopoden,' 1841. Grenacher, "Zur Entwickelungsgeschichte der Cephalopoden," ('Zeitschrift für Wiss. Zoologie,' 1876). Lankester "Observations on the development of the Cephalopoda." ('Quarterly Journal of Micr. Science,' 1875.)

The *Cephalopoda* are divided into two very distinct groups, the *Tetrabranchiata* and the *Dibranchiata*.

The *Tetrabranchiata* possess an external chambered siphunculated shell. The terminal chamber is much larger than any of the rest, and the body of the animal can be almost completely retracted into it. When, as in the only existing genus, *Nautilus* * (Fig. 130), the shell is coiled into a flat symmetrical spiral, its apex lies on the anterior face of the body, and the outermost chamber, into which the whole body can be retracted, is consequently posterior to the axis of the helix. In *Nautilus*, the brachial processes are short, and possess no acetabula such as exist in the *Dibranchiata*, but the margins of the foot are produced externally into a sort of sheath, which, in front, has the form of a broad hood with a tuberculated surface; while, at the sides, it is divided into many processes of unequal lengths. Behind, the halves of the sheath are separated throughout the greater part of their length by a wide interval, but are united above by a thick muscular isthmus. The central portion of the sheath is a broad triangular hood-like plate, the apex of which is free. It contains two long narrow cavities, each of which lodges a tentacle. The tentacle consists of a slender stem, on which are set a great number of transverse plates, in such a manner that the axis of the stem passes through the centre of the plates. The anterior and lateral regions of the hood are completed by two narrower processes, each of which contains a similar tentacle, and the lateral portions of the sheath are formed by sixteen or seventeen smaller tentaculiferous processes, the surfaces of which are more or less distinctly annulated. When the sheath is opened out, there is seen to be attached to its inner surface, on each side, close to the re-entering angle between it and the lip which surrounds the beak, and along the line of junction of the lateral part of the sheath with the isthmus, a

* Owen, 'Memoir on the Pearly Nautilus,' 1832. Van der Hoeven, 'Annales des Sciences Naturelles,' 1856. Keferstein, in Bronn's 'Klassen u. Ordnungen.'

thin free quadrate lobe which carries twelve tentacles. The isthmus joins the posterior edges of these *outer tentaculiferous lobes*, as well as those of the two halves of the sheath, and it exhibits on its anterior, or inner surface, a broad area beset with delicate close-set curved laminæ. Two other similar, but much thicker, *inner tentaculiferous* lobes, which also carry twelve tentacles, lie between these and the lip. They are quite free from the outer

Fig. 130.

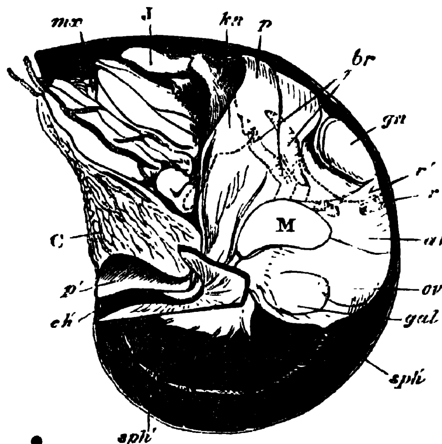


Fig. 130.—*Nautilus pompilius*, female. C, hood; *mx*, jaws; J, funnel; *p*, *p'*, mantle; *br*, branchiæ; *gn*, nidamental gland; *r'*, *r*, position of the renal appendages; *ann*, horny ring; *u*, shell muscle; *ov*, ovary; *gal*, oviducal gland; *sph'*, siphuncle; *ch*, black part of the shell under the mantle *p'*, *kn*, process of the cartilaginous skeleton into the funnel. (After Keferstein.)

tentaculiferous lobes, and unite with the sheath only above and behind. Like the halves of the sheath, these two lobes are united behind by a thick isthmus, the surface of which presents a number of parallel longitudinal laminæ. The beak, which is hidden by the sheath and the lobes, is surrounded by the thin circular lip already mentioned, the free margin of which is papillose. Besides these, there is a

short conical tentaculiferous process above the pedunculate eye, and another below it. In the male, the internal tentaculiferous lobes are wanting, and the outer tentaculiferous lobes are divided into two portions, an anterior which bears eight, and a posterior with four, tentacula. On the left side, the four tentacles of the posterior division have undergone much modification, and are converted into a peculiar organ termed the *spadix*, which bears a discoidal follicular gland upon its outer surface. There is thus a kind of hectocotylisation in the *Tetrabranchiata*.

The margins of the united epipodia are not united into a tubular funnel. They constitute a muscular membrane, narrow on the anterior face of the body, but becoming wide, and folded in such a manner that its posterior edges overlap, behind.

The mantle has a broad anterior fold, which covers the anterior convexity of the shell, and the region which it thus invests is black. The pallial chamber does not extend for more than three-fifths of the length of the body, and is therefore much less deep than in the *Dibranchiata*. The anus opens in the middle line on the posterior wall of the pallial cavity, close to its junction with the anterior wall. The four branchiæ are attached, two on each side of the anus, to the posterior wall of the branchial chamber, and the inner branchia is shorter than the outer. The nidamental glands, composed of numerous vertical lamellæ, partly covered by a fold of the lining membrane of the pallial cavity, are situated on the posterior wall of that cavity, almost midway between its union with the anterior wall and its free edge. The paired renal chambers lie immediately above them also, in the posterior wall of the pallial cavity.

The buccal mass is very large, its length amounting to one-third that of the body. The apices of the great horny beaks are obtuse, and are coated with a calcareous deposit. The œsophagus dilates into a wide crop and is separated by a constriction from the stomach, the chitinous lining of which is thick and ridged. The pyloric cæcum

is small and rounded, and the intestine makes two bends upon itself before reaching the anus. Salivary glands appear to be wanting, unless certain glandular bodies placed within the buccal mass should be of this nature.

The liver is a loosely racemose gland, divided into four lobes, and is lodged in the anterior part of the perivisceral cavity. There is no ink-bag; and there are no branchial hearts. The quadrate systemic heart is situated on the left side of the posterior face of the body, close to the junction of the posterior with the anterior wall of the pallial cavity. It receives four branchio-cardiac veins; and, attached to it, is a pyriform sac, which, according to Keferstein, opens into the pallial cavity.

The cartilaginous skeleton supports the pedal and parieto-splanchnic ganglia, but does not encircle the gullet, or roof over the cerebral ganglia. Two long processes of the skeleton pass into the funnel and give attachment to its muscles. Two large shell muscles are attached to it; and, passing upwards and outwards, are inserted into oval chitinous patches visible on the outer surface of the mantle, and connected together by a thin ring of the same substance (the *annulus*) which encircles the mantle.

The oviduct does not arise directly from the sac in which the ovary is lodged, but from a distinct chamber, into which the ovarian sac opens. A large albumen gland pours its secretion into the ovarian sac. The vas deferens similarly takes its origin, not from the sac of the testis, but from a smaller chamber communicating therewith. The commencement of the vas deferens is enlarged and glandular. Nothing is known of the development of the *Tetrabranchiata.*

The only existing representatives of the *Tetrabranchiata* are the different varieties of "pearly nautilus" (*Nautilus pompilius*), which are found in the Southern seas, living at the bottom at a considerable depth. The genus is one of the oldest in existence, since it is traceable through the whole series of fossiliferous rocks as far back as the Silurian epoch.

Along with it, in the Palæozoic formations, occur numerous closely allied forms, which differ from *Nautilus* mainly in the different curvature (*Lituites, Gyroceras, Trochoceras*) or straightness (*Orthoceras, Gomphoceras*) of the shell, and in the varying position, proportions, and degree of calcification of the siphuncle.

In the middle of the Palæozoic strata (Devonian), Tetrabranchs (*Ammonitidæ*) appear, in which the margins of the septa are strongly bent, whence their edges appear as zigzag transverse lines, folded into *lobes* and *saddles*, when the outer layer of the shell is worn away (*Goniatites, Ceratites*); and, in the Mesozoic epoch, the lobes and saddles become extremely complicated, while the shells may be straight, simply curved, or bent, or turbinated (*Ammonites, Baculites, Turrilites*). The *Ammonitidæ* are extraordinarily numerous in the Mesozoic epoch, but no trace of them has been found in tertiary or quaternary formations.

Associated with *Ammonites*, and not unfrequently lodged in the terminal chamber of the shell, are the so-called *Aptychi*. These are plates of a shelly substance, three-sided, with rounded off angles, and applied together by their straightest edges so as to resemble bivalve shells. They consist of two layers, an inner and an outer, of which the inner presents lines of growth, concentric with the angle of each plate which is situated on that side of its broad end which is applied to its fellow. The outer layer is composed of many laminæ, and is traversed by pores. Its free surface frequently presents longitudinal ridges. The heart-shaped plates, undivided by a suture, which are found in some *Goniatites* and *Ammonites*, are termed *Anaptychi*.

The *Aptychi*, when undisturbed, occupy the middle of the posterior wall of the terminal chamber of the Ammonite, and have their bases towards its mouth. Nothing is certainly known as to the nature of the *Aptychi* or *Anaptychi*.*

* See the discussion of this question by Keferstein, in Bronn's 'Thierreich.'

In the *Dibranchiata*, the margins of the foot are produced into not fewer than eight, nor more than ten, arms, which are provided with *acetabula* or suckers. Each acetabulum is a sessile or stalked cup, from the bottom of which rises a plug, which nearly fills the cup, but can be retracted by the action of muscular fibres attached to it. When the margins of the acetabulum are applied to any surface, and the plug is retracted, a partial vacuum is created, and the acetabulum is caused to adhere to the surface by atmospheric pressure. The edges of the acetabula are frequently strengthened by chitinous rings, and these may be serrated (Fig. 124, B), and are sometimes produced into long curved hooks.

The margins of the united epipodia are not only folded inwards, but coalesce so as to give rise to a tubular funnel, through which the water taken into the branchial sac for respiratory purposes is ejected. Very often, a valve which prevents the flow of water back into the mantle cavity is developed within the funnel. There are two branchiæ, and the anus terminates between them in the anterior wall of the branchial sac, on which also the nidamental glands are situated. The apices of the horny beaks are acutely pointed, and not ensheathed in calcareous matter. The liver is usually a compact mass. A peculiar gland, which secretes an extremely dark fluid—the so-called ink,—and has the form of an oval or pyriform sac (the *ink-bag*), with a long duct which opens into, or close to, the rectum, is lodged sometimes in the liver, sometimes further back (Fig. 126, I). The ink is ejected when the animal is alarmed, and gives rise to a dark cloud in the water, by which its retreat is covered. There are two branchial hearts.

The eye is lodged in an orbit and is provided with a lens. The cartilaginous endoskeleton forms a ring surrounding the gullet and enveloping the principal ganglia. There is usually an internal pallial shell. It may be chambered and siphunculated, but in this case, the last chamber is small and hardly larger than the others.

The *Dibranchiata* are divided into the *Octopoda* and the *Decapoda*. The *Octopoda* have eight arms, and possess no

pallial shell. But, in the female of one genus (*Argonauta*, the "paper Nautilus," Fig. 131), the extremities of the anterior pair of arms are greatly expanded, and, being turned back over the mantle, secrete an elegant shelly structure which covers the body, and serves for the attachment of

Fig. 131.

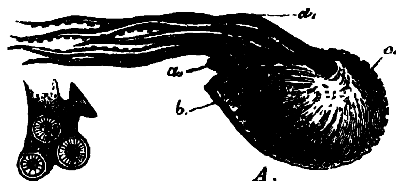


Fig. 131.—*Argonauta argo.*—A, female with the expanded arms in their natural position, embracing the shell *b*; *d*, the other six arms; *a*, the funnel. B, acetabula.

Fig. 132.



Fig. 132.—*Argonauta argo*, male, with the *Hectocotylus*-arm attached.

the eggs. In this genus, and in some other Octopods (*Octopus carina*, *Tremoctopus violaceus* and *T. Quoyanus*), the male is very much smaller than the female, and gives rise to a *Hectocotylus*.

In *Argonauta argo* (Figs. 132, 133) it is the third arm on the left side which becomes thus modified. At first, it has the form of a sac, within which the slender terminal part of the arm is coiled up (Fig. 133, B). The sac splits to give exit to the latter (Fig. 132), and its two halves reunite on the outer face of the base of the arm to form a chamber, which becomes filled with spermatophores in a manner not yet understood. During sexual union, the arm

Fig. 133.

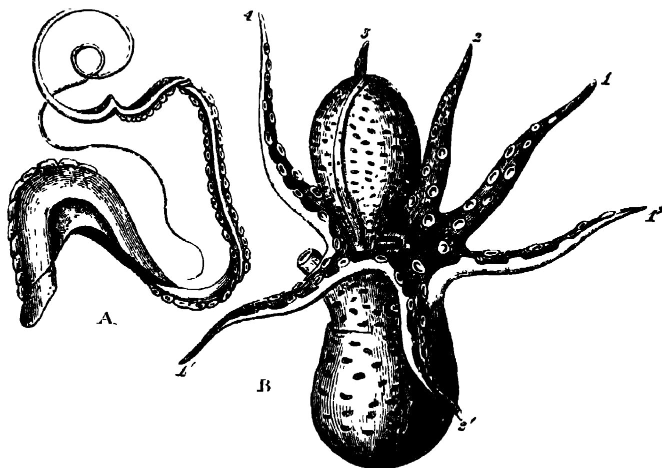


Fig. 133.—*Argonauta argo.*—B, male, with the hectocotylised arm enclosed in its sac; 1, 2, 3, 4, the other arms of the right side; and 1′, 2′, 4′, those of the left side. A, the hectocotylus detached.

thus charged with semen is detached and left in the mantle cavity of the female (Fig. 133, A). When first discovered, it was regarded as a parasite and termed *Trichocephalus acetabularis* by Delle Chiaje, while the corresponding body found in an *Octopus* was called *Hectocotylus octopodis* by Cuvier.

In *Tremoctopus*, it is the third arm on the right side

which becomes the *Hectocotylus*. In other *Octopods** one or other arm is peculiarly modified, but does not become detached, or serve as a receptacle for the spermatophores.

The *Decapoda* have ten arms, two of which are usually much longer than the rest, and can be protruded from, or retracted into, sockets. The acetabula have horny rims, which may take on the form of hooks.

Hectocotylisation does not go further than a modification of the form of one of the arms. There is always an internal shell, which is either a *pen*, a *sepiostaire*, a *phragmocone*, or a combination of the latter with a pen.

The *Teuthidæ*, or Squids, are characterised by possessing a pen. This is a lamellar chitinous body, strengthened by one or more longitudinal ridges, which lies in a sac lodged in the anterior wall of the body, by the lining membrane of which it is secreted. The posterior end of the pen is commonly broad, and its sides may be infolded so as to form a conical cup (*Ommastrephes*).

In the *Sepiadæ*, or Cuttle-fishes, the sepiostairé, or "cuttle bone," which occupies the same position (Fig. 125, *sh*), is composed of a broad plate answering to the pen, and likewise infolded at its apex so as to give rise to a short cone, but calcified. On the inner face of this plate, a great number of delicate calcified laminæ, connected by numerous short columns, form a spongy tissue, which is full of air.*

In the *Spirulidæ*, represented by the solitary genus *Spirula*,† which is among the rarest of animals in museums, though its shells are found piled up in countless millions on the beaches of the islands of the Pacific, the shell is spirally

* Steenstrup, "Die Hectocotylen-bildung bei *Argonauta* und *Tremoctopas* erklärt durch Beobachtungen ähnlicher Bildungen bei den Cephalopoden." ('Archiv für Naturgeschichte,' 1856.)

† The planes of the superimposed parallel laminæ form an acute angle with that of the principal plate of the sepiostaire. The connecting columns are placed perpendicularly to the laminæ between which they are interposed, and may be simple or branched. When the young *Sepia* leaves the egg, the sepiostaire already contains air.

† Owen, 'Zoology of the Samarang,' 1848.

Fig. 134.

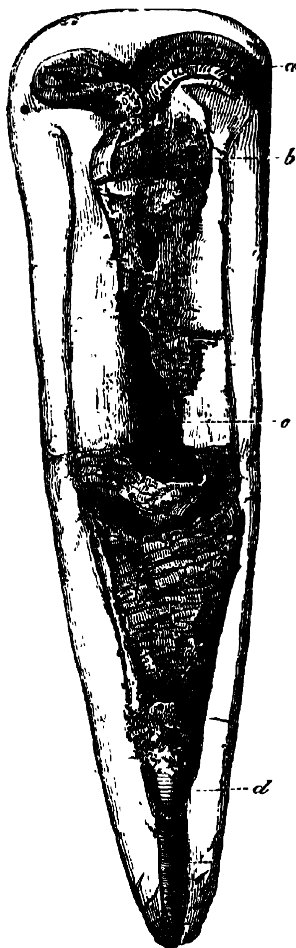


Fig. 134.—*Belemnites*, with the remains of the body of the animal. (From a specimen in the Museum of Practical Geology.)—*a*, arms with hooks; *b*, head; *c*, ink-bag; *d*, phragmocone; *e*, guard.

coiled and divided by septa, perforated by a siphuncle, into chambers. The last chamber of this phragmocone, however, is no larger than its predecessor, and the shell is held in position by lateral processes of the mantle, which are united over it, and probably represent the walls of the sac in which the shell was primitively formed. The last chamber of the shell lies in front of the axis of the helix; the shell is therefore coiled in the opposite direction to that of *Nautilus*.

In certain extinct genera (*e.g. Spirulirostra*), a shell, like that of *Spirula*, is enclosed in a dense and laminated pointed sheath, like the hinder end of a sepiostaire, or of the pen of an *Ommastrephes*.

In the *Belemnitidæ* (Fig. 134), which abounded in the Mesozoic epoch, but have been extinct since that time, a straight phragmocone is enclosed within a more or less conical calcified laminated structure, the *guard* or *rostrum*, which is continued forwards into a variously-shaped, usually lamellar, *pro-ostracum*. The pro-ostracum and the rostrum together represent the pen in the *Teuthidæ*.

The rare specimens of *Belemnitidæ* in which the fossilised soft parts are retained, show that the arms were provided with hooks, and that there was a large ink-bag.*

The genus *Acanthoteuthis*† (*Belemnoteuthis*, Pearce)—one of the *Belemnitidæ*, in which the guard is almost rudimentary, while the pro-ostracum is large and penlike—occurs in the Trias, and is the earliest known Dibranchiate Cephalopod. The ordinary *Belemnitidæ* abound from the Lias to the end of the Mesozoic period, after which they disappear. The *Sepiadæ* first appear in the latter half of the Mesozoic epoch; while the *Teuthidæ* are represented by genera closely allied to existing forms (*Teuthopsis, Belemnosepia*) as early as the Lias.

* Huxley, "The structure of Belemnites." ('Memoirs of the Geological Survey of the United Kingdom,' 1864.)

† Owen, "A description of certain Belemnites," &c. ('Phil. Trans.' 1844.)

CHAPTER IX.

THE ECHINODERMATA.

THE Echinoderms are exclusively marine animals. They are always provided with a skeleton, composed of calcareous spicula, which commonly unite into networks, and give rise to definite skeletal plates. These generally become connected with one another by joints or sutures, but sometimes remain distinct. A more or less spacious peritoneal cavity separates the walls of the body from those of the alimentary canal. The nervous system, in those Echinoderms in which it has been most satisfactorily made out, presents a ring, which surrounds the gullet, and gives off radiating longitudinal cords. A remarkable system of vessels, termed *ambulacral*, which also form a ring around the gullet, is highly characteristic of the *Echinodermata*. The most conspicuous and familiarly known Echinoderms —the Star-fishes (*Asteridea*), Brittle-stars (*Ophiuridea*), Sea-urchins (*Echinidea*), and Feather-stars (*Crinoidea*)—have a marked radial symmetry; similar parts, usually to the number of five, being arranged around a central axis; and the body is spheroidal, discoidal, or stellate. The Sea-cucumbers and Trepangs (*Holothuridea*) are elongated and vermiform; but the radial symmetry is still traceable in the arrangement of the oral tentacula, the nervous, and the ambulacral systems. It is to be remarked, however, that, in many Echinoderms, the radial symmetry, even in the adult, is more apparent than real; inasmuch as a median plane can be found, the parts on each side of which are disposed symmetrically in relation to that plane. With a few exceptions, the embryo leaves the egg as a bilaterally

symmetrical larva, provided with ciliated bands, and otherwise similar to a worm-larva, which may be termed an *Echinopædium*. The conversion of the Echinopædium into an Echinoderm is effected by the development of an en-

Fig. 135.

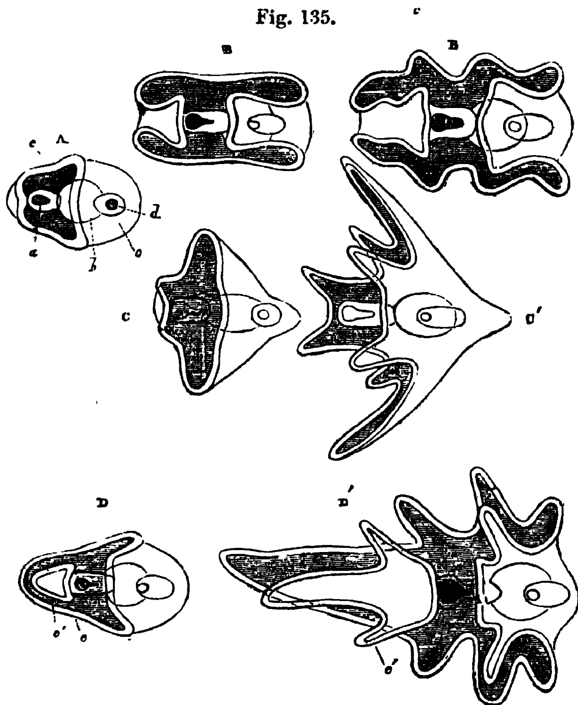


Fig. 135.—Diagram exhibiting the general plan of the development of the *Echinoderms* (after Müller).—A, common form whence the vermiform Holothurid (B, B') and the pluteiform Ophiurid or Echinid (C, C') larvæ are derived; D, D', younger and more advanced stages of the Asterid (*Bipinnaria*) larvæ; *a*, mouth; *b*, stomach; *c*, intestine; *d*, anus; *e*, ciliated band; *e'*, second or anterior ciliated circlet of *Bipinnaria*.

terocœle, and its conversion into the peritoneal cavity and the ambulacral system of vessels and nerves; and by the

metamorphosis of the mesoderm into radially disposed antimeres, the result of which is the more or less complete obliteration of the primitive bilateral symmetry of the animal.

1. The HOLOTHURIDEA. The study of the structure of the Echinoderms may best be commenced with the members of this division, which, in many respects, deviate least from such worms as the *Gephyrea*.

In the *Synaptæ*, for example (Fig. 136), the body is greatly elongated and cylindrical, the mouth being placed at one end, and the anus at the other. The oral aperture is situated in the centre of a circle of tentacula, and the gullet leads from it to an alimentary canal, without marked distinction of stomach and intestine, which extends through the body, and is connected by a mesentery with the parietes of the latter. The wall of the alimentary canal presents external circular, and internal longitudinal, muscular fibres, and its cavity is lined by a cellular endoderm.

The body-wall, or *perisoma*, consists of an external cellular ectoderm, covering a layer of connective tissue within which are circular and longitudinal muscular fibres. The latter are disposed in five bands, attached anteriorly to a corresponding number of the pieces of a calcareous ring which surrounds the gullet (Fig. 136, E). The separate ossicles which compose this ring are usually ten or twelve in number, and the five to which the longitudinal muscles are attached are notched or perforated for the passage of the ambulacral nerves, which proceed from the circum-œsophageal nerve to the parietes of the body.

The integument contains numerous perforated, flat, calcareous plates, to which protruding anchor-like hooks of the same substance are attached (Fig. 136, F). According to Semper, these anchor-like bodies are developed in special sacs with an epithelial lining.*

A spacious peritoneal cavity lies between the parietes

* See, on this and all points relating to the structure of the *Holothuridea*, the beautiful monograph by Semper: "Reisen im Archipel der Philippinen." ('Wissenschaftliche Resultate,' Bd. i.: *Holothurien*.)

of the body and the alimentary canal, and the cells which line it are more or less extensively ciliated. Pedunculated ciliated cups are attached to the mesentery.

The circular vessel of the ambulacral system surrounds the gullet below the calcareous ring (Fig. 136, E, *h*). Posteriorly, it gives off various cæcal prolongations, which depend freely into the peritoneal cavity. Some of these—the *Polian vesicles*—are mere cæca; but, in addition, there are one or more tubular prolongations, the perforated extremities of which are invested by a calcareous network, and are termed the *madreporic canals*. Through the openings in the free end of the madreporic canal, the interior of the ambulacral system communicates with the peritoneal cavity. Anteriorly, the circular vessel gives off branches to the tentacula. These pass between the calcareous ring on the outer side, and the anterior end of the alimentary canal and the nerve ring, on the inner side. As each enters its tentacle, it dilates and sends down a short cæcal prolongation on the outer side of the calcareous ring. The ambulacral vessels are filled with a fluid containing numerous nucleated cells.

Contractile vessels, which accompany the intestine and lie on opposite sides of it, filled with a similar corpusculated fluid, seem, notwithstanding the difference in their contents, to represent the pseud-hæmal vessels of the Annelids. These vessels do not extend into the parietes of the body.

The nervous system consists of a ring which lies superficial to the circular water-vessel, and from which five principal equidistant cords proceed. These pass through the apertures or notches in the circum-œsophageal plates already mentioned, and each proceeds along the middle line of one of the longitudinal muscular bands, to the opposite extremity of the body.

The ambulacral nerves appear to be hollow; or perhaps it would be more correct to regard them as thickenings in the wall of a neural canal, as they are in the *Asteridea*.*

* According to Greef ("Ueber den Bau der Echinodermen," 3te Mittheilung, Sitzungsberichte der Gesellschaft zu Marburg, 1872), another canal lies superficial to the ambulacral nerve in

The genital gland is single, and opens near the oral end of the body, in the line of the attachment of the mesentery. The branched cæcal tubuli of which it is composed contain both ova and spermatozoa, so that the *Synaptæ* are hermaphrodite. In the majority of the *Holothuridea*, however, the sexes are distinct.

In other *Holothuridea*, the skeleton may attain a much greater development, and even take the form of conspicuous overlapping plates (*Psolus*). Moreover, the circular vessel of the ambulacral system not only gives origin to Polian vesicles, madreporic canals, and tentacular vessels, but five canals proceed from it, pass through holes or notches in those circum-œsophageal plates to which the longitudinal muscles are attached, together with the nerves, and run backwards, along the centre of the area occupied by these muscles, on the deep or inner side of the longitudinal nerve. These are the *radial ambulacral vessels.* In the higher *Holothuridea*, each radial ambulacral vessel gives off many lateral branches; these enter contractile processes of the body-wall, which subserve locomotion, and are the *ambulacral feet, suckers,* or *pedicels.* In accordance with the disposition of the ambulacral vessels, the pedicels are usually disposed in five longitudinal bands, which are the *ambulacra.* Sometimes (*Psolus*) the pedicels are suppressed in two of the five ambulacra, and the other three are disposed upon a flattened surface upon which the animal creeps.

In the higher Holothurids, the intestine terminates in a distinct cloaca, into which two hollow ramified organs, which lie in the perivisceral cavity, open. The ramifications of one of these are received between the meshes of a special plexus of the pseud-hæmal vessels. Water is taken into, and expelled out of, the cloaca and these appendages, which, doubtless, subserve an excretory function, and are commonly called *respiratory trees.* It seems probable that the

the *Holothuridea*; and represents the ambulacral groove of the starfishes. Teuscher, "Beiträge zur Anatomie der Echinodermen" ('Jenaische Zeitschrift,' 1876), however, maintains that this superficial canal is an artificial product.

Fig. 136.

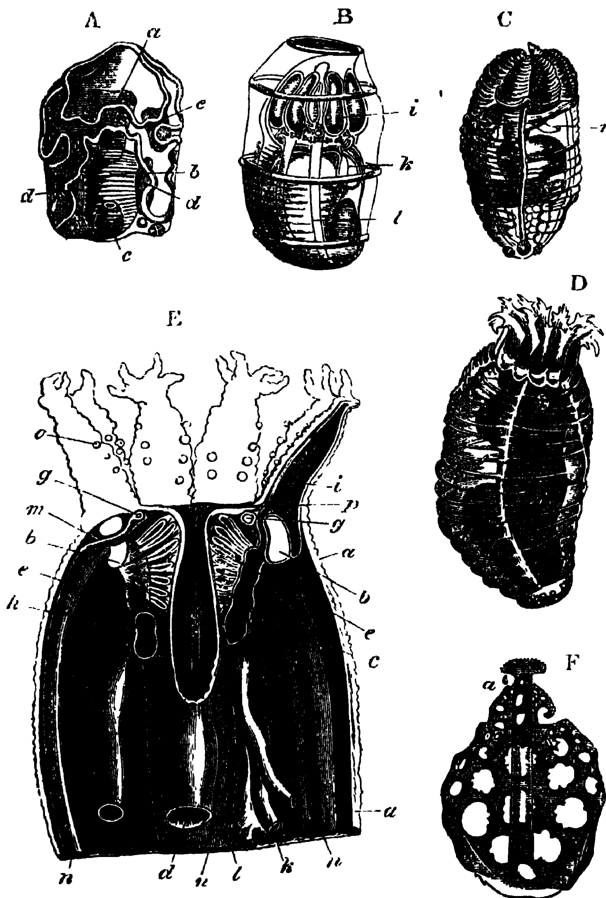


Fig. 136.—*Synapta digitata* and *inhærens* (after Baur).*

A. Larva with the bilateral ciliated band, and wheel-shaped calcareous plates. Ventral view. *a*, mouth and gullet; *b*, stomach;

* "Beiträge zur Naturgeschichte der *Synapta digitata*." ('Nova Acta,' xxxi., 1864.)

c, intestine and anus; *d*, sacs of the enterocœle (sausage-shaped bodies) at the sides of the stomach; *e*, rudiment of the ambulacral vascular system. B. Further advanced condition of the larva in which the oral aperture is obsolete (the so-called "pupa-stage"), and the cilia are arranged in zones. *i*, tentacula; *k*, Polian vesicle; *l*, the longitudinal muscles of the body-wall. C', a young *Synapta*, in which the ciliated zones have disappeared; with its five tentacles and the wheel-shaped calcareous bodies at its hinder end. *m*, the madreporic canal which now opens into the cavity of the body. D, a young *Synapta inhærens* with anchor-shaped calcareous spicula, except at the hinder end of the body, where they are small and polygonal. E. Longitudinal section of the anterior end of the body of an adult *Synapta digitata*. *a*, perisoma with the longitudinal muscles and radial nerve trunks; *b*, calcareous plates which surround the gullet; *c*, tentacular canals; *d*, œsophagus; *e*, radiating muscles of the pharynx; *g*, divided ends of the circum-oral nerve; *h*, circular ambulacral vessel with Polian vesicle; *i*, cavity of a longitudinally divided tentacle, into which a tentacular canal opens; *k*, generative cæca; *l*, mesentery with the dorsal blood-vessel; *m*, 'auditory vesicle' on the radial nerve; *n*, longitudinal muscles; *o*, tentacular pedicels; *p*, oral disk. F. Calcareous plate and anchor of *Synapta inhærens*.

ultimate branches of these organs open directly into the perivisceral cavity.*

The *Cuvierian organs* are simple or branched appendages of the cloaca, the function of which is unknown. The interior of these organs is occupied by a solid substance, sometimes of a viscid nature. In some *Holothuridea*, the anal aperture is provided with a circlet of calcareous plates.

In many of the higher Holothurids the pseud-hæmal vascular system attains a great complexity, and its branches not only extend over the alimentary canal, but, as has been said above, closely embrace one of the branched excretory organs.

The most aberrant form of this group at present known is the genus *Rhopalodina*. According to Semper, the body is flask-shaped, and at the narrow end of the flask are two apertures. One of these—the mouth—is surrounded by ten tentacula; the other, which is the anal aperture, is encircled by ten papillæ, and by as many calcareous plates. A spacious cloacal cavity, provided with excretory organs, traverses the neck of the flask, and opens by the anal

* Semper, *loc. cit.* Heft iv., p. 133.

aperture. The gullet is surrounded by a ring of ten calcareous plates. The genital duct is situated between the cloaca and the gullet. Ten ambulacra diverge from the centre of the enlarged aboral end of the body, and extend, like so many meridians, to near the commencement of the neck of the flask. In correspondence with each ambulacrum is a longitudinal muscular band; and it is an especial peculiarity of *Rhopalodina* that five of these are attached to the anal circlet, and five to the circum-œsophageal circlet. Until, however, it has been shown that the circular ambulacral vessel encloses the cloaca, as well as the œsophagus—which is highly improbable,—it is justifiable to assume that the anus of *Rhopalodina* is really, as in the *Crinoidea*, interradial in position.

The development of the *Holothuridea* is extremely instructive. Yelk-division gives rise to a vesicular morula, which undergoes invagination, and becomes converted into an oval ciliated gastrula. The opening of invagination becomes the anus, while a mouth and gullet are produced by an invagination of the ectoderm, near the anterior end of the body, which unites with and opens into the blind end of the endodermal sac, or archenteron. The completed alimentary canal is thus composed of a gullet, a rounded stomach, and an intestine; and the cilia of the ectoderm usually become restricted to a single band, bent upon itself, though its general direction is transverse to the axis of the body (Fig. 135, B; Fig. 136, A). At a subsequent period, this single band may be replaced by a series of hoops of cilia (Fig. 136, B). According to Kowalewsky* the embryo of *Pentacta doliolum* does not become ciliated at all, and that of *Psolinus* passes from the condition in which the cilia are dispersed over the surface, directly into one in which it is provided with five zones of cilia, between two of which the mouth opens. In this condition it singularly resembles the embryo of *Comatula*. And, indeed, in the further advanced condition of the *Psolinus*, the oral end of the body, surrounded by triangular cal-

* 'Mém. de l'Acad. de St. Pétersbourg,' 1868.

careous plates, within which the tentacles take their origin, has a striking resemblance to the oral end of the young Pentacrinoid larva of *Comatula.*

The peritoneal cavity and the ambulacral vessels take their origin,* in a very remarkable manner, from the archenteron, before the œsophageal invagination reaches it. The anterior part of the archenteron gives off a cæcal process, which, becoming a sac, is constricted off from the archenteron as what Salenka terms a *vaso-peritoneal vesicle.* This vesicle changes its position to the left side of the alimentary canal, and then sends a narrow duct-like diverticulum towards the dorsal region of the ectoderm, which eventually coalesces with the latter, the cavity of the diverticulum opening on the exterior by a rounded pore. The vaso-peritoneal vesicle now divides into two portions, one of which, the *ambulacral sac*, remains connected with the exterior by the duct, and constitutes the foundation of the whole of the ambulacral system of vessels; while the other, the *peritoneal sac*, gives rise to the peritoneum. The former becomes five-lobed, grows round the gullet, and gives rise to the tentacular and ambulacral canals with the Polian vesicle, or vesicles; while the duct, detaching itself from the dorsal wall, becomes the madreporic canal.

The latter divides into two vesicles, which arrange themselves at the sides of the stomach. The stomach takes on a more cylindrical shape, and these vesicles become the "sausage-shaped bodies" (würstförmige Körper), observed by Müller (Fig. 136, A). They gradually increase in size, and growing round the alimentary canal, unite above and below it. Thus a cylindrical cavity with a double wall is formed, between the endoderm and the ectoderm. The inner wall of the cavity applies itself to the alimentary canal, and aided by the mesoblastic cells which appear to be developed from the endoderm, becomes the muscular

* See Metschnikoff, "Studien über die Entwickelung der Echinodermen und Nemertinen" ('Mém. de l'Acad. de St. Pétersbourg, xiv., 1869); and especially the very satisfactory memoir of Salenka, "Zur Entwickelung der Holothurien" ('Zeitschrift für Wiss. Zoologie,' 1876).

and peritoneal coat of that viscus; while the outer wall, attaching itself to the ectoderm, or to the mesoblastic cells which line it, is, with them, converted into the muscular and peritoneal investment of the parietes of the body. The interspace between the two is the peritoneal cavity.

Fig. 137.

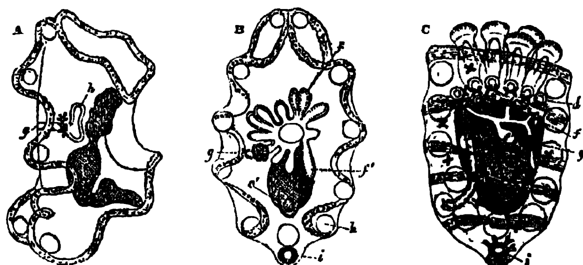


Fig. 137.—Development of a Holothurid (after Müller).—A, Early condition of the larva (*Auricularia*); *g*, the dorsal pore of *h*, the ambulacral sac; B, later stage; *c'*, intestine; *g*, dorsal pore; *f*, *f'*, circular ambulacral vessel with its prolongations; *i*, calcareous body; C, young *Holothuria* with circular ciliated bands; *g*, madreporic canal; *f'*, Polian vesicle.

In the meanwhile, the body of the embryo elongates, the tentacula are developed around the mouth, the ciliated bands disappear, and the Holothurid Echinoderm is complete.

Thus it is clear that the peritoneal cavity of the Holothurid is an enterocœle, and that it answers to the perivisceral cavity of *Sagitta*, or of the *Brachiopoda*; and further, that the ambulacral vessels are also modifications of the enterocœle. Moreover, it is obvious that the structures which are developed between the enterocœle and the ectoderm and endoderm, answer to those which are evolved from the mesoblast in other animals; and that the adult Echinoderm stands in the same relation to the *Echinopædium* as an Annelid does to its embryo; the adult form being due to the peculiar arrangement of the parts developed from the mesoblast. No part of the Echinopædium

is cast off in the course of the development of the *Holothuridea.*

2. The Asteridea.—A Star-fish is comparable to a Holothurid, the ambulacra of which are restricted to its oral half, flattened out so as to have a very short axis; while its equatorial diameter is greatly increased, and produced in directions corresponding with each ambulacrum. The result would be a disk, having the form of a pentagon, or of a five-rayed star, with ambulacra only on that face of the disk which bears the mouth. Hence the *ambulacral,* and the opposite, or *antambulacral,* faces are of equal extent.

Most *Asteridea* are like five-rayed stars, but some are pentagonal disks (*Goniaster*), and some few (*Solaster*) have more than five rays. In *Brisinga,* the rays are much more different from the disk than usual, and the genus thence acquires an outward resemblance to an Ophiurid.

All the *Asteridea* are provided with a skeleton made up of plates or thick rods, composed of a dense calcareous network. A deep groove, radiating from the mouth to the end of the ray, marks the position of each ambulacrum, and the sides of this groove are supported by two series of *ambulacral ossicles,* which meet and articulate together in the middle line or roof of the groove. The ambulacral nerve and canal lie superficial to these ossicles. There are no oral tentacula.

The five-rayed body of the commonest of British Star-fishes,* the Fivefinger (*Uraster,* or *Asteracanthion, rubens*), presents an *oral face,* in the centre of which the mouth is placed, and an opposite or *aboral face.* The hardly-discernible anal aperture is situated not exactly in the centre of this face, but close to it. The mouth, which varies very much in size, lies in the middle of a soft membranous *oral disk.* A deep furrow, the *ambulacral groove,* occupies the middle of the oral surface of each ray, and is nearly filled

* Compare Hoffmann, "Zur Anatomie der Asteriden." ('Niederländisches Archiv,' Bd. ii. 1874.)

by contractile sucker-like pedicels, with circular discoidal ends, apparently arranged in four longitudinal series. The deepest part of the groove is at its central end, where its lining passes into the oral membrane. The shallowest part is at its distal end, where it terminates against a median projection, the peduncle of the eye, on the aboral side of which is the single median *ocular tentacle*. Lines drawn from the mouth along each ambulacrum are termed *radii*, and the regions occupied by the ambulacra are said to be radial. The parts of the body situated between the ambulacra are *interradial*. The lateral walls of the ambulacral grooves of adjacent ambulacra unite at the circumference of the oral disk, and give rise to five *interradial angles*. On one side of the aboral face of the centre of the body, between the origins of two of the rays, and therefore interradial in position, is an oval or somewhat pentagonal, slightly convex, porous plate, the surface of which is covered with narrow meandering grooves. This is the *madreporic tubercle* or *madreporite*.

The perisoma, or wall of the body, upon the aboral face, and upon the sides of the rays, is everywhere covered with short *spines*. In the intervals between these, groups of delicate membranous tubuli, which are closed at their free ends, project. Small two-pronged pincer-like bodies, the *pedicellariæ*, are attached to the spines and to the perisoma between them, and during life are seen to twist about and snap.

The perisoma presents, externally, a cellular ectoderm, provided with a thin cuticle, which bears numerous cilia. Beneath this lies a mesoderm, containing connective and muscular elements, in which the calcareous structures which constitute the skeleton are lodged. On the inner side of the perisoma, a ciliated epithelium lines the perivisceral cavity.

The separate elements of which the skeleton is composed may be divided into three groups: the *ossicula*, which, joined end to end and united by connective and muscular tissues, constitute the chief framework of the body; the *spines*,

attached to the ossicula by ligamentous fibres at one end, and free at the other; and the calcareous structures contained in the *pedicellariæ*. On the antambulacral wall of the body, the ossicula are elongated rods of very unequal lengths, united together in such a manner as to leave polygonal, rounded, or elongated, meshes. The sides and roof of each ambulacral groove, however, are bounded by two series of regularly disposed and similar *ambulacral ossicles*, which lean against one another in the middle line above, diverge so as to enclose the ambulacral groove, and, at their outer ends, abut upon thick short *adambulacral* ossicles, which lie at the sides of the groove (Fig. 139, D).

Between every two ambulacral ossicles in the same half of the ambulacrum there is a canal, formed by the junction of notches in the oral and distal faces of the two ossicles. Consequently there is a half-pore on the oral, and another half-pore on the distal face of each ossicle. The half-pore on the oral face is always internal in position to the half-pore on the distal face, and, as the part of the ambulacral ossicle which lies between the two is thin, the row of pores, though it is really single and bent in a sharp zigzag, appears at first sight to be double. The ducts which connect the ambulacral vesicles with the pedicels, traverse these pores; and the comparatively large and very flexible and extensile pedicels are thus so closely packed together, that they appear to form a double row, on each side of the middle of the ambulacrum.

At the circumference of the oral disk, the ossicles of the ambulacra, diminished in size and closely united together, form a pentagon, the angles of which answer to the ends of the ambulacral grooves, round the œsophagus. The conjoined outer ends of the pair of ambulacral ossicles nearest the mouth project on the oral face, outside the buccal membrane, as five vertical crests, armed with strong spines, which are beset with pedicellariæ. In correspondence with these, five falciform folds of the perisoma, more or less calcified, project into the cavity of the body. They are interradial in position, and extend up to the aboral wall.

Their inner edges are free, and look towards the stomach; with one of them, the madreporic canal and the sinus which accompanies it, are closely connected.

The *spines* are more or less moveably united with the ossicula, but there are no such regular joints as are met with in the *Echinidea*. The *pedicellariæ* are supported upon short flexible peduncles. The skeleton of each consists of two blades articulated with a basal piece. From the centre of this very strong adductor muscles proceed to the inner faces of the blades, and weaker fibres, attached to the exterior and to the outer faces of the bases of the blades, act as divaricators.

The gullet opens into a wide stomach produced into five large *cardiac sacs*, the walls of which are subdivided into many sacculi. Each cardiac sac is radial in position, and may extend a short way into the cavity of the arm to which it corresponds. On the aboral side of these sacs, the alimentary canal suddenly narrows, and then dilates again into a shallow, but wide, pentagonal *pyloric sac*, the angles of which are produced into five tubes. Each of these passes along the middle of the aboral face of a ray, and divides into two branches, which run parallel with one another through half or two-thirds the length of the ray, and end blindly. The branches give off numerous cæcal dilatations, arranged in pairs on opposite sides, and these hang down into the cavity of the ray. The edges of the pentagonal pyloric sac and the aboral faces of its sacculated branches are connected by mesenteric folds with the aboral perisoma. The oral faces of the cardiac sacs are similarly connected by pairs of mesenteric folds with the sides of the corresponding series of ambulacral ossicles. The aboral face of the pyloric sac presents an aperture closed by projecting valvular folds, which leads into the short tubular intestine. The latter terminates in a minute anal pore, situated nearly in the centre of the aboral face of the body. The intestine receives the duct of a cæcum divided into two main branches, each of which has many minor subdivisions. If the animal, having

its mouth downwards, is divided into two halves, by a vertical plane passing through the mouth, the central point of the aboral face, the madreporic tubercle, and the middle line of the ray opposite to the tubercle; and if this ray is anterior; then the anus opens into the left posterior interradial space, and the cæca lie partly in this and partly in the left anterior interradial space.

The nervous * and vascular systems of the Star-fish are so closely related to one another that they may be best considered together, and as there is least difficulty in making out their arrangement in the ambulacra, the study of them may be commenced in this region.

When the suckers of an ambulacrum are carefully cut away, a longitudinal ridge is seen to lie at the bottom of the groove between their bases. This ridge is the *ambulacral nerve.* Followed to the apex of the ray, it ends upon the eye and its tentacle; in the opposite direction, it reaches the oral disk, at the periphery of which it divides, and skirting the margins of the disk, joins the branches formed by the bifurcation of the adjacent ambulacral nerves, thus giving rise to a subpentagonal ring round the mouth.

The eye † is a thick cushion-like expansion of the ectoderm continuous with the ambulacral nerve. In it are imbedded many clear oval bodies surrounded by pigment, which appear to represent the crystalline cones of a compound eye.

The tentacle which lies on the aboral side of the eye, resembles one of the pedicels in structure, but has no terminal sucker; its function appears to be tactile.

In a good transverse section of one of the arms or rays of the Star-fish, the nerve is seen to be a band-like thickening of the ectoderm, the cells of which have become peculiarly modified, but which is continuous laterally with the ordinary ectodermal covering of the pedicels. This band-like nerve constitutes the superficial wall of a canal,

* See Wilson, "The nervous system of the Asterida" ('Trans. Linnean Society,' 1862), and the later contributions of Professor Teuscher cited below.

† Conf. Haeckel, 'Zeit. für Wiss. Zoologie,' 1860.

which extends through the whole length of the ambulacrum and may be termed the *ambulacral neural canal*. It is divided by a longitudinal septum. At its oral end, as has been seen, each ambulacral nerve, when it reaches the oral membrane, divides into two divergent branches, which unite with the corresponding branches of the other ambulacral nerves to form the oral ring. Answering to the latter is a wide *circular neural canal*, into which the ambulacral neural canals open.

In the transverse section of the arm, a second and much larger canal is seen to lie between the conjoined ends of the ambulacral ossicles and a strong septum, containing transverse fibres, which separates it from the neural canal. This is the *radial canal* of the ambulacral system of vessels. At its oral end it opens into the *circumoral ambulacral vessel* which lies close to the ossicles to which the margins of the oral membrane are attached. From opposite sides of the radial canal, short branches are given off, which pass between the ambulacral ossicles, and each opens into the neck of a relatively large sac, with muscular walls (*ambulacral vesicle*), which lies on the aboral face of the ambulacral ossicles in the interior of the ray. The neck of the ambulacral vesicle passes in the opposite direction into one of the pedicels. Thus the ambulacral vessel communicates with the cavities of all the pedicels on the one hand, and with the cavity of the circumoral ambulacral vessel on the other. Five pairs of small eminences, consisting of cæca which open into the circumoral vessel, are seated upon it; and from one part of it, opposite one of the interradial falciform folds already mentioned, springs a canal, which, taking a sinuous course, passes to the aboral face and terminates beneath the madreporic tubercle; this is the *madreporic canal*. It is not a simple tube, but, as Sharpey first observed, its walls are doubly involuted so as partially to obstruct its cavity, and it is strengthened by annular calcifications. The pores of the madreporic tubercle place the cavity of the madreporic canal in communication with the exterior, whence it follows

that the cavities of the whole ambulacral system must be directly accessible to the sea-water in which the Star-fish lives. The madreporic canal is invested by the lining membrane of the peritoneal cavity. This incloses a sinus, which accompanies the madreporic canal, and into the interior of which a fold projects.

There is no great difficulty in ascertaining the existence of the structures which have now been described, and all anatomists are agreed as to the nature of the ambulacral system. But whether the neural canals are to be considered as a special system of blood-vessels, and the sinus which accompanies the madreporic canal, a heart, as is usually assumed, appears to me to be very doubtful.* I am disposed to think, in fact, that not only these canals, but the circular, or rather, pentagonal vessel which has been described as situated on the aboral face of the body, around the anus, giving off various branches to the viscera and communicating with the so-called heart, are mere subdivisions of the interval between the parietes of the body and those of the alimentary canal, arising from the disposition of the ambulacral vessels and that of the walls of the peritoneal cavity; both of which, as their development shows, are the result of the metamorphosis of saccular diverticula of the alimentary canal, which have encroached upon, and largely diminished, the primitive perivisceral cavity which exists in the embryo.

The peritoneal cavity of the body and rays is filled with

* Since Tiedemann's time, the presence or absence of a blood-vascular system in the Starfishes has been alternately asserted and denied. The recent investigations of Greef, "Ueber den Bau der Echinodermen" ('Marburg Sitzungsberichte,' 1871-2), Hoffman (l. c.), and of Teuscher, "Beiträge zur Anatomie der Echinodermen" ('Jenaische Zeitschrift,' Bd. x.), are in favour of the existence of the 'anal ring,' and of an extensively ramified system of canals, connected with it and with the neural canals. But it does not appear to me that the facts, as they are now known, justify the assumption that these canals constitute a distinct system of blood-vessels. Injections show that all these canals communicate with the ambulacral vessels, and with the exterior, by means of canals in the madreporic tubercle which open partly outwards, partly into the madreporic canal, and partly into the sinus which accompanies it, and communicates with the circumoral neural vessel.

a watery corpusculated fluid; a similar fluid is found in the ambulacral vessels, and probably fills all the canals which have been described. The corpuscles are nucleated cells, which exhibit amœboid movements; and the fluid so obviously represents the blood of the higher animals, that I know not why the preposterous name of "chylaqueous fluid" should have been invented for that which is in no sense "chyle," though, like other fluids of the living body, it contains a good deal of water. As the cavities of the tubular cæca of the perisoma communicate freely with the general cavity, and their walls share in the general ciliation of the lining of the cavity, it is very probable that they may subserve the function of respiration.

The genital glands are situated in pairs, interradially, at the junction of the body with the rays. Each gland is divided into a number of elongated processes, the common base of which is attached to the face of one of the interradial septa, while the processes project freely into the cavities of the arms. According to Hoffmann and Greef, the inner cavities of the genital processes are filled when the vascular system is injected. It is possible, therefore, that the genital glands are merely processes of the mesodermal layer, in the walls of which the genital products are developed; in which case there would be a close approximation between the genital glands of the Star-fishes and those of the Crinoids. According to Greef, the external openings of the genital glands are visible in *Uraster*, in the breeding season; in other Star-fishes, they are conspicuous in the interradii of the aboral face of the body. In *Luidea*, *Ophidiaster* and some other genera, the glands extend far into the interior of the arms, and Prof. G. O. Sars * has pointed out that, in *Brisinga endecacnemos*, the genitalia are numerous distinct glands, arranged in two series, one on each side of the middle line of the central half of

* 'Researches on the Structure and Affinity of the genus *Brisinga*,' 1870. In this important memoir the author proves that *Brisinga* is a true Asterid, and not, as has been supposed, a transitional form between the *Asteridea* and the *Ophiuridea*.

each ray. Each of these ovaries or testes has a separate aperture.

In some Star-fishes, as in some Holothurids, the embryo passes into the Star-fish form without any free larval stage. But, more usually, an Echinopædium is formed in the same way as in the Holothurians, though it presents differences in the arrangement of its ciliated bands, and especially in their prolongation into numerous lobes or narrow processes. as in the remarkable form originally named *Bipinnaria*. (Fig. 135, D D′, and Fig. 138.) It has no calcareous skeleton.

Fig. 138.

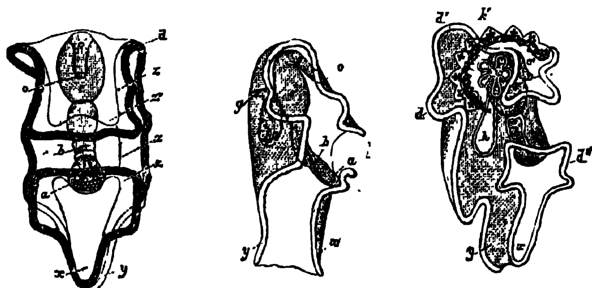


Fig. 138.—A young *Asterid* larva (*Bipinnaria*, after Müller).—A, ventral; B, lateral views of larva (*Bipinnaria*); C, *Bipinnaria* with rudiment of the Star-fish, *a*, mouth; *b*, œsophagus; *c*, stomach; *c*′, intestine; *o*, anus; *x*, ventral; *y*, dorsal side of the anterior end of the body; *d*, *d*′, ciliated bands; *h*, cæcal diverticulum forming the rudiment of the ambulacral vascular system, and opening externally by the pore *g*.

According to the observations of Prof. A. Agassiz,* which have been confirmed by Metschnikoff and Greef, the ambulacral vessels commence as diverticula of the stomach, which, becoming detached from the alimentary canal, give rise to the peritoneal cavity, and to all the substance

* "Embryology of the Star-fish." ('Contributions to the Natural History of the United States,' V. 1864.) The species, the development of which is described in this important memoir, are *Asteracanthion pallidus* and *A. berylinus*.

of the body between the endoderm and the ectoderm.* A portion of one of these diverticula, however, separates itself from the rest, opens externally by a pore, and becomes metamorphosed into the ambulacral vessels. But this ambulacral diverticulum does not surround the gullet, and consequently a new mouth is developed in the centre of the ambulacral ring. The larval mouth and gullet are abolished, and the greater part of the body of the Echinopædium is separated from that portion which contains the stellate Echinoderm. The latter results from the metamorphosis of the mesoderm, which is modelled upon the different divisions of the enterocœle, and encloses the middle portion of the alimentary canal.†

The OPHIURIDEA.—The brittle Stars, though they resemble the ordinary Star-fishes in form, differ essentially from them, not only in the structure of their skeleton, but in the characters of the Echinopædium. The ambulacra are confined to the oral aspect of the body, so that, as in the *Asteridea*, the ambulacral and oral, the antambulacral and the aboral surfaces, respectively coincide. The mouth is situated in the centre of the oral face, but no grooves radiate from it along the ambulacra, which are covered by a series of plates of the skeleton. The alimentary canal is a simple gastric sac without cæca, and has no intestine or anus. In contradistinction from the Star-fishes, the prolongations of the peritoneal cavity into the rays are very narrow.

The typical *Ophiuridea* possess a very complete calcareous skeleton; which, on the body and on the exterior of the rays, has the form of plates. On the body, the disposition of these varies much; but five of them, which are situated

* Probably independently developed mesoblastic cells contribute to the formation of the mesoderm as in the Holothurids.

† Greef (*l.c.*) has worked out the development of *Uraster* (*Asteracanthion*) *rubens*, the larval form of which resembles the *Bipinnaria* and *Brachiolaria* of Helsingfors, described by Müller. Parthenogenesis appears to occur in this Star-fish.

interradially in the neighbourhood of the mouth, are often larger than the others, and are termed *scuta buccalia.*

Each ray contains an internal solid axis, composed of a single series of quadrate *axial* ossicles (Fig. 139, C, *a*), each consisting of two lateral halves united by a longitudinal suture and articulated together by tenon and mortice joints upon their terminal surfaces. Each of these ossicles (which are sometimes termed *vertebral*) is surrounded by four plates; one median and antambulacral (Fig. 139, C, *b*), two lateral (Fig. 139, B, *c*) and one median and super-ambulacral (Fig.

Fig. 139.

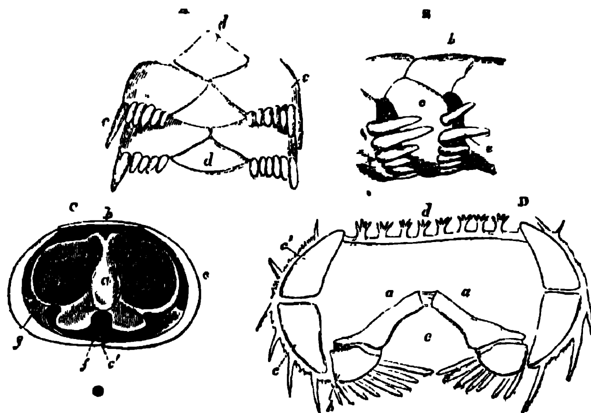


Fig. 139.—A, ventral, B, lateral, views of a ray of *Ophiura texturata* (after Müller). C, transverse section. *a*, axial or "vertebral" ossicle of ray; *b*, antambulacral plate; *c*, lateral plate; *d*, ventral or superambulacral plate. D, section of a ray of an Asterid, *Astropecten aurantiacus* (after Gaudry). *a*, ambulacral or "vertebral" ossicles; *b*, adambulacral ossicles; *c*, *c*', marginal ossicles; *d*, paxillæ of antambulacral surface.

139, A, *d*). The lateral plates may meet in the middle line on both the ambulacral and the antambulacral faces. Between the lateral plates are the apertures by which the pedicels make their exit. The oral aperture is surrounded by five *oral angles*, each of which consists of five pieces. The two

constituents of the axial ossicle which lies at the oral end of a ray become moveably articulated with one another, while each ankyloses with an interambulacral piece. Transverse muscles connect the two interambulacral pieces, the oral edges of which are articulated with a long narrow plate, the *torus angularis* (Fig. 140, *f*). The free surface of the *torus angularis* lies in the walls of a sort of vestibule in front of the mouth. A number of short flat processes, the *palæ angulares*, are articulated with it and moved by special muscles. They doubtless perform the function of teeth. Rudimentary representatives of the calcareous ring of the *Holothuridea* and of the parts of the lantern of the *Echinidea* exist as delicate calcareous plates, which lie on the circular ambulacral vessel. The latter is usually provided with cæcal appendages, or *Polian vesicles*. The madreporic canal ends on the surface of one of the *scuta buccalia*; the radial ambulacral vessels run in the arch between the axial ossicles and the super-ambulacral plates. The nerve lies superficial to the super-ambulacral vessel, but is also covered by the super-ambulacral plate. A neural canal lies between the nerves and the ambulacral vessels. The pedicels are tentaculiform, and have no vesicles at their bases. The genital glands are lodged in the disk, and pour their products into the peritoneal cavity, which communicates freely with the exterior by vertically elongated apertures placed interradially on its margins.* According to Metschnikoff, *Ophiolepis squamata* is hermaphrodite.

The early conditions of the embryos of most *Ophiuridea* are similar to those of other Echinoderms, and acquire the characteristic bilateral ciliated zone; but in some, the embryo does not become an *Echinopædium*, but passes directly into the adult condition. Thus Krohn discovered

* Müller, "Ueber den Bau der Echinodermen" (Abh. Berl. Akad. 1853); Teuscher (l. c.); Simrock, "Anatomie und Schizogonie der *Ophiactis virens*" ('Zeitschrift für Wiss. Zoologie,' 1876). The latter writer describes numerous apparently cæcal diverticula of the circular ambulacral canal, and of the necks of the Polian vesicles (*vasa ambulacralia cavi*) which traverse the peritoneal cavity in all directions.

that the embryo of *Ophiolepis ciliata* is developed within the body cavity of the parent, to which it adheres by a kind of pedicel. Where an *Echinopædium* stage exists, the larva is a *Pluteus* (Fig. 135, C C'). The dorsal wall of the body of the embryo exhibits a median conical outgrowth; along the course of the ciliated band symmetrically disposed processes are developed; and these outgrowths are supported by a calcareous skeleton, which is also bilaterally symmetrical. Metschnikoff* has made the interesting observation that in an Ophiurid (probably *Ophiothrix fragilis*) the whole system of perivisceral and ambulacral cavities

Fig. 140.

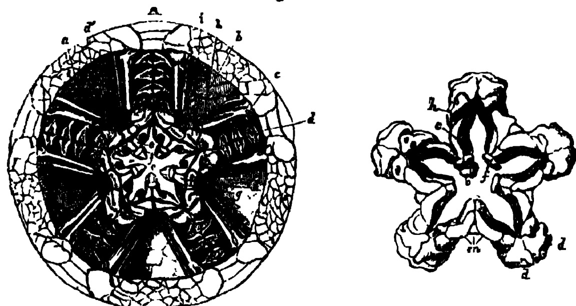


Fig. 140.—A, *Ophiolepis ciliata*, oral skeleton from within (after Müller).—*a*, dorsal marginal plates; *b*, ventral plates; *d*, vertebral ossicles; *e*, interambulacral pieces of oral angle; *f*, torus angularis; *g*, apertures for oral tentacles; *h*, position of nervous collar; *i*, impression of circular ambulacral vessel; *k*, orifice in the first ambulacral plate for the tentacular branch of the oral vessel; *o*, palæ angulares. B, *Astrophyton*, oral skeleton seen from within (after Müller): *m m*, peristomial plates; other letters as in A.

arises from two bodies, one situated on each side of the gullet, which are solid, though it is possible that they may primitively have been hollow diverticula of the archenteron. Two cellular masses become detached from these bodies, apply themselves to the sides of the stomach, and are con-

* "Studien über die Entwickelung der Echinodermen und Nemertinen." ('Mém. Acad. St. Pétersbourg,' 1869.)

verted into disks, from which the parietal and visceral walls of the peritoneal cavity take their origin. The rest of the solid body on the left side of the gullet acquires a vesicular character, opens by a dorsal pore, and grows round the gullet, to give rise to the circular ambulacral vessel. The other solid body disappears. The mouth of the Echinopædium becomes that of the Ophiurid.

It cannot be doubted that these solid bodies take their origin, in the same way as in other Echinopædia, from the hypoblast; and thus the question arises, how far does the mesoblast thus formed differ from that which arises by the mere outgrowth of cells from the hypoblast, as in the Dog-fish, and how far does this case tend to render it probable that a schizocœle is only a modification of an enterocœle?

The ECHINIDEA.—An ordinary Sea-urchin is comparable to a Holothurid, with the body distended into a more or less globular form, and with a skeleton in the form of regular plates arranged in meridional series; those plates which correspond with the ambulacral vessels being superficial to the latter, and consequently perforated by the canals which pass from the ambulacral vessels to the pedicels.

In the *Echinidea*, as for instance in the ordinary *Echinus* or Sea-urchin, the perisoma round the mouth (*peristome*) is usually strengthened for some distance by irregular oral plates. In addition, ten rounded plates are placed in pairs close to the lip; these support as many pedicels and are perforated by the canals of the latter. A much smaller space around the anus (*periproct*) is similarly protected by anal plates. The rest of the body is supported by a continuous wall made up of distinct, more or less pentagonal plates, usually firmly united by their edges, which is called the *corona*. Of these plates there are twenty principal longitudinal series, constituting the great mass of the corona; and ten single plates, which form a ring around its aboral or apical margin. The twenty series of longitudinal plates are disposed in ten double series—

five ambulacral, and five inter-ambulacral—alternating with one another throughout the circumference of the corona. Each double series of plates presents a zigzag suture in the middle line, formed by the alternating arrangement of the triangular extremities of its component elements. The sutures between the respective series of ambulacral and interambulacral plates, on the other hand, are less obvious

Fig. 141.

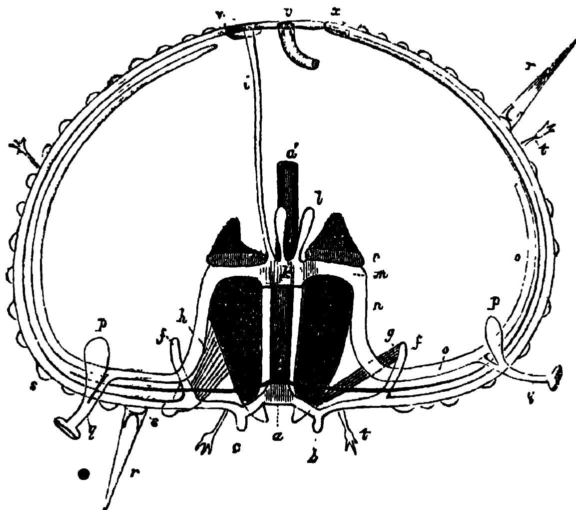


Fig. 141.—Diagram exhibiting the relations of the different systems of organs in an *Echinus*.—*a*, mouth; *b*, teeth; *c*, lips; *d*, alveoli; *e*, falces; *f*, auriculæ; *g*, retractor, and *h*, protractor muscles of lantern; *i*, madreporic canal; *k*, circular ambulacral vessel; *l*, polian vesicle; *m*, *n*, *o*, ambulacral vessel; *p*, pedal vesicle; *q*, *q*, pedicels; *r*, spine; *s*, tubercle to which it is articulated; *t*, pedicellariæ; *u*, anus; *v*, madreporic tubercle; *x*, ocular spot.

and more straight. Each ambulacral plate is subdivided by a greater or less number of sutures, which traverse it obliquely, into a corresponding number of minor plates; and these, inasmuch as they are perforated by the canals

or pores, which give exit to the two vessels whereby each pedicel is placed in communication with its basal vesicles and with the ambulacral vessel, are called *pore plates.* Throughout the greater part of the length of an ambulacrum of the common *Echinus sphæra* (Fig. 142, A) each ambulacral plate is thus divided into three pore plates, traversed altogether by six pores or short canals. The outer openings of these canals are arranged close together in pairs upon little excavated shield-shaped elevations, or *umbones,* sculptured on the outer or interambulacral half of the face of the ambulacral plate; but their inner extremities are much wider apart. A pore plate, or subdivision of the ambulacral plate, thus corresponds with each pair of pores, and therefore with each pedicel. Lovén * has shown that the pore plates are the primitive ambulacral ossicles in the *Echinoidea.* At its apical extremity, in fact, the ambulacrum is composed of only two small ossicles which meet in the middle line. Each of these primitive ambulacral ossicles is perforated by a single or double pore for the pedicel which it bears. But as, in the course of the growth of the corona, new primitive ambulacral ossicles are added between the ocular plate and those already formed, the latter shift towards the oral end of the ambulacrum and grow, in correspondence with the larger space which they have to fill. But they grow unequally; and while all retain their primitive connexions with the adjacent interambulacral plates, some lose, while others retain their median union with the corresponding ossicles of the same ambulacrum. The former, therefore, are, as it were, pushed away from the middle line by the union of their encroaching predecessors and successors. Groups of the primitive ambulacral plates, thus modified, enter into close union, and constitute the complex ambulacral plates of the fully developed ambulacrum.

In the genus *Cidaris,* the primitive ambulacral plates enlarge, but do not coalesce into secondary ambulacral

* "Etudes sur les Echinoïdées." ('Kongl. Svenska Vetensk-Akad. Handlingar,' Bd. II, 1875.)

plates; hence the distinction between ambulacral plates and pore plates vanishes. The ambulacral plates are continued on the peristome to the margins of the mouth, and here they become somewhat altered in form and their edges overlap.

In the living genus *Asthenosoma*, and in certain extinct *Echinidea* (*Lepidocentrus*, *Echinothuria*), the plates of the corona are loosely united and overlap one another; while, in the extinct palæozoic *Perischoechinidæ*, there are more than two series of interambulacral plates, those in the middle of each interambulacrum being hexagonal.

Fig. 142.

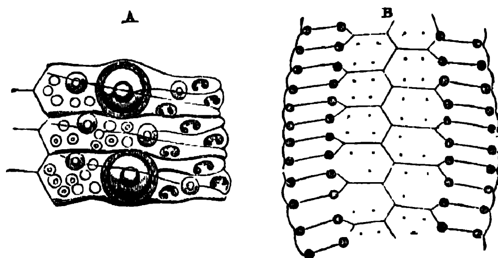


Fig. 142. (After Müller.)—A. Three ambulacral plates of *Echinus sphæra*, exhibiting the sutures of the pore plates of which each ambulacral plate is composed. B. Part of the petaloid ambulacrum of a Clypeastroid.

In *Echinus*, the apical extremities of the ambulacra abut upon the five smaller of the ten single plates which surround the periproct. Each of these is perforated, and supports the eyespot; it is thence called an *ocular plate*. The apical extremities of the interambulacra, on the other hand, correspond with the five larger plates, which alternate with the ocular plates, and, like them, are perforated. The aperture is, however, larger, and constitutes the exit for the generative products. One of these five *genital* plates is larger than the others, and presents a peculiar porous convex surface, which is the madreporic tubercle or *madre-*

porite. The latter is therefore interambulacral in position, as in the Star-fish.

Comparison with the elongated Echinoderms shows that the madreporite lies in the right anterior inter-radius of the sea-urchin, so that the anterior ambulacrum is that which lies to the left of the madreporite, when the latter is directed forwards. In consequence of being able to distinguish this odd or anterior radius, it is possible in any of the *Echinidea*, to separate the three anterior ambulacra, as the *trivium*, from the two posterior, the *bivium*; and in the fossil genus, *Dysaster*, this separation of the ambulacra into trivium and bivium exists naturally. Müller has pointed out that in all the flattened *Echinidea*, with a special ambulatory surface, the latter is formed by the bivial ambulacra and interambulacra, while, in the similarly modified *Holothuridea*, the animal rests upon the trivium.

Within the circle formed by the genital and ocular plates the periproct presents a variable number of calcifications, of which one, the *anal plate*, is larger than the rest. The anus lies excentrically, between this plate and the posterior margin of the periproct.

With the exception of certain palæozoic forms (*Palæchinus*), the composition of the skeleton of the *Echinidea* is always essentially similar to that which has just been described; but the form of the body and the relative positions of the anal and oral apertures may vary very much. In the *Echinoida* (*Cidaris*, *Echinus*) the body is spheroidal, and the oral and anal apertures are opposite and central, or very nearly so. In the *Clypeastroida* (*Clypeaster*, *Echinocyamus*) the form of the body varies from a spheroidal to an excessively flattened and even lobed shape. The mouth remains central, but the anus varies in position, from the apical surface to the margin, or even to the oral surface, as in *Echinocyamus*. In the remaining division of the *Echinidea*, the *Spatangoida* (*Spatangus*, *Amphidotus*, *Ananchytes*), the form is usually a somewhat depressed oval, and both the oral and the anal apertures are excentric. The madreporite and the genital and ocular plates, on the other

hand, remain in the centre of the aboral region in all the *Echinidea*.

The ambulacra present important variations in the three divisions of the *Echinidea*. In the *Echinoida* they are *homogeneous*, presenting the same composition from their oral to close to their apical extremities, and having the pores and pedicels similar throughout. Furthermore, the ambulacra are widest in the middle, and taper gradually to each extremity (*Echinus*), or are of nearly the same size from one end to the other (*Cidaris*).

In many *Clypeastroida*, on the contrary, the oral and the apical portions of each ambulacrum differ very widely, or are *heterogeneous*. The apical moiety is usually very wide in the middle and tapers to a point marginally, where it joins the oral portion. Hence there is an appearance of five petals diverging from the apex; and such ambulacra are called *petaloid* (Fig. 142, B). In the oral portions of the ambulacra, on the contrary, the pores are either scattered widely over the ambulacral, and sometimes over the inter-ambulacral, plates, forming *pore-areæ*; or they are arranged in bands which ramify over the inter-ambulacral as well as the ambulacral plates, giving rise to what Müller has termed *pore fasciæ*. In the *Spatangoida* (Fig. 143) the ambulacra commonly present the same heterogeneous character; but the oral portions are not arranged in fasciæ; and it not unfrequently happens that the anterior ambulacrum becomes more or less abortive, so that only four petals are obvious on the apical surface, instead of five.

The growth of the shell of the *Echinidea* is effected in two ways; partly by addition to the circumference of the existing plates, partly by the interpolation of new ambulacral and inter-ambulacral plates at the apical end of each series between it and the ocular or genital plate, as the case may be. New plates are never added to the oral extremity of the corona proper.

The surface of the plates of the corona in the *Echinidea* is covered with minute rounded elevations, or *tubercles*, to which are articulated the spines so characteristic of the

group. The tubercle may be either simple or marked by a central pit, into which and a corresponding pit on the head of the spine a ligament of attachment is inserted. Furthermore, capsular muscular fibres connect the neck of the spine with the base of the tubercle, and effect the varied movements of which the organ is capable. The spines of the *Echinidea* vary very much in form and size, from the close-set velvety pile of *Scutella*, or the delicate spoon-shaped blades of *Amphidotus*, to the long-pointed lances of *Echinus* and the great clubs of *Cidaris*. Even on the same Echinoderm the spines may, as in the two latter genera, vary very much in appearance; and it becomes necessary to distinguish those large ones which form a continuous series from one end of an ambulacrum or inter-ambulacrum to the other, as *primary* spines, from the other less complete *secondary* and *tertiary* series.

Lovén * has drawn attention to the existence in all the *Echinidea*, except *Cidaris*, of certain minute spheroidal bodies, rarely more than $\frac{1}{100}$ of an inch long, which he terms *sphæridea*. They occur upon the ambulacral plates, and especially upon those nearest the mouth. Each contains a calcareous and more or less dense and glassy skeleton, which is articulated with a corresponding tubercle as if it were a miniature spine. In some genera, these *sphæridea*, to which Lovén ascribes a sensory function (probably auditory), are sunk in fossæ of the plate to which they are attached.

Scattered among their spines, the *Echinidea* possess *pedicellariæ*, which are usually provided with long slender stems, terminating in oval heads, divided into three jaw-like processes. The latter are strengthened by calcareous ossicles, which articulate with an ossicle contained in the basal part of the head, and a calcareous rod is usually developed in the stem.

In the *Spatangoida*, when the skeleton is cleaned, its surface is, in many cases (*Amphidotus*, *Brissus*, *Spatangus*), marked by one or more symmetrical bands of close-set,

* 'Etudes sur les Echinoïdées,' 1875.

minute tubercles (Fig. 143, *e*, *f*, *g*). During life, slender spines are attached to these tubercles, the calcareous skeleton of

Fig. 143.

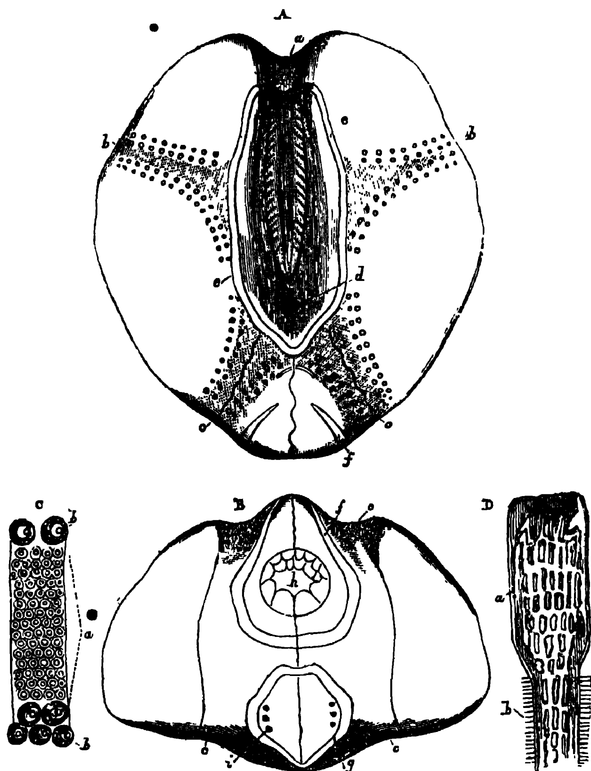


Fig. 143.—*Amphidotus cordatus.*—A. Viewed from above. B. From behind. *a*, *bb*. Trivium, or anterior and anterolateral ambulacra. *cc*. Bivium, or posterolateral ambulacra. *d*. Madreporic tubercle, surrounded by the genital apertures. *e*. Intra-petalous *semita*. *f*. Circum-anal *semita*. *g*. Sub-anal *semita*. *h*. Anus. *i*. Intra-semital pores of bivial ambulacra. C. Semita magnified. *a*. Semital tubercles. *b*. Ordinary tubercles. D. Semital spine. *a*. Terminal enlarged, non-ciliated portion. *b*. Ciliated stem.

which is clothed with a thick coat of integument, which suddenly enlarges at the apex (Fig. 143, D); long and close-set cilia cover the shaft of the spine, while no such structures exist on the terminal enlargement. These bands of peculiarly modified spines are called *semitæ* or *fascioles*. *Semitæ* lie beneath and surround the anus in some genera, and are called *sub-anal* and *circum-anal*; others surround the outer extremities of the petaloid ambulacra, and are termed *peripetalous*, or, when they encircle the inner terminations of their ambulacra, *intrapetalous* (*Amphidotus*) (Fig. 143, A, B).

If we turn to the interior of the shell of the *Echinidea*, we find in the *Echinoida*, that ambulacral, or sometimes (*Cidaris*) interambulacral, plates of the oral margin of the corona are produced into five perpendicular perforated processes, which arch over the ambulacra, and are called the *auriculæ*.

Besides these, processes are developed from the ambulacral plates in *Cidaris*, which form a sort of wall on each side of the ambulacral canal, but do not arch over it. In *Clypeaster*, similar processes form complete arches; and in the flattened Clypeastroid, *Scutella*, the oral and apical walls of the corona are united together by calcareous trabeculæ, so that the cavity of the body is restricted to a very small space.

The *Spatangoida* present neither *Auriculæ*, nor other internal processes.

In the *Echinidea*, the œsophagus is usually distinct, but, beyond a cæcal diverticulum in some cases, there is no further differentiation of the alimentary canal, which is disposed spirally around the walls of the corona, and attached thereto by a mesentery.

In the *Echinidea*, the oral skeleton attains its highest development in the so-called "Aristotle's lantern" of the Sea-urchins (Fig. 144, B, C, D).

This apparatus consists of five hollow, wedge-shaped, calcareous pieces—the *alveoli* (Fig. 144, B, *a*), each of which is composed of two halves united together in the

middle line, while each half again consists of a superior

Fig. 144.

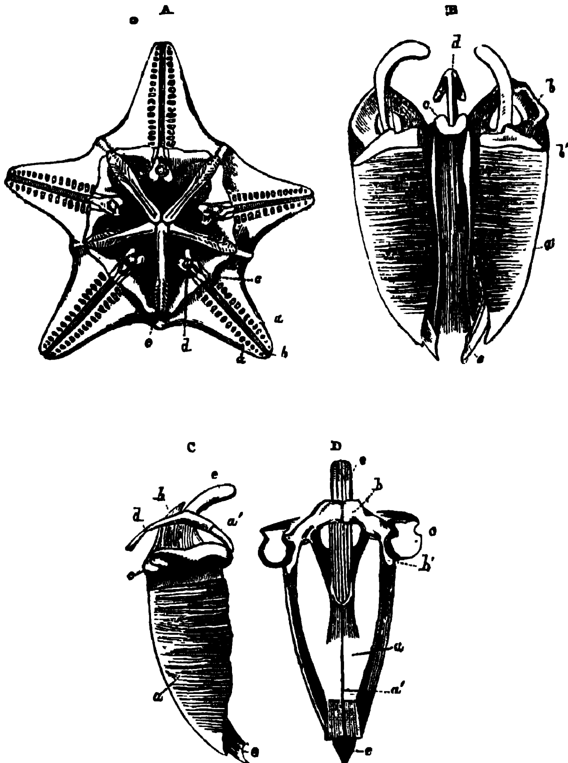


Fig. 144.—A. Dentary apparatus of a *Clypeastrid* (after Müller).—*a.* Alveolus. *d.* Rotula. *e.* Tooth. B, C, D. Dentary apparatus (Aristotle's lantern) of *Echinus sphæra.* B. Two of the five chief component parts of the lantern apposed and viewed laterally. C. Lateral view, and D. back view of a single part. *a.* Principal piece of alveolus. *a'.* Suture with its fellow. *b.* Epiphysis. *b'.* Suture of epiphysis with principal piece. *c.* Rotula. *d.* Radius or compass. *e.* Tooth.

epiphysis, and an inferior principal portion, united together. Each alveolus serves as the socket for a long tooth (*e*), shaped somewhat like the incisor of a Rodent, harder externally than internally, so as always to develope a sharp edge with wear. The tooth constantly grows from its upper extremity, while its lower half becomes united with the wall of the alveolus. The five alveoli, if fitted together, form a cone, the applied surfaces of which are united by strong transverse muscular fibres, while superiorly, the epiphyses of each pair of alveoli are connected by long radial pieces—the *rotulæ* (*c*) articulated with their edges. To the inner extremity of each rotula, finally, a slender arcuated rod, presenting indications of a division in the middle of its length, is articulated, and, running outwards parallel with the rotula, terminates in a free bifurcated extremity. This is the *radius* (*d*).

Altogether, then, the Lantern consists of twenty principal pieces—five teeth, five alveoli, five rotulæ and five radii; of which the alveoli are again divisible into four pieces each and the radii into two, making a total of forty pieces. In their normal position, it must be remembered that the alveoli and teeth are interambulacral, while the radii and rotulæ are ambulacral. Besides the inter-alveolar muscles already described, this complex apparatus has protractor muscles arising from the interambulacral region of the oral edge of the corona, and inserted into the upper part of the alveoli; slender oblique muscles, with a similar origin, but inserted into the radii; transverse muscles connecting the radii together; and retractor muscles arising from the arches of the auriculæ, and inserted into the oral ends of the alveoli.

A similar, but less complex, oral skeleton exists in most *Clypeastroida* (Fig. 144 A), but nothing of the kind has yet been discovered in the *Spatangoida*.

In the *Echinidea*, the circular ambulacral vessel lies between the œsophagus and the alveoli, and is usually provided with five sacculated polian vesicles. There is a single madreporic canal, membranous in *Echinus*, but calcareous

in *Cidaris*, which extends nearly in the axis of the body from the circular vessel to the madreporic tubercle. Five radial vessels run up the middle of the inner surface of the ambulacral plates, which they reach by passing from the circular canal, outwards, beneath the rotulæ, when these exist; next, downwards, external to the inter-alveolar muscles; and then, outwards, through the arches of the auriculæ: these give off branches on each side to the pedicels, the bases of which open into large ambulacral vesicles. The circular ambulacral vessel of the *Spatangoida* has no polian vesicles, and no vesicular appendages; in the Clypeasters there are many vesicular appendages, but no polian vesicles. In most *Echinoida*, all the pedicels are expanded into sucking-disks at their extremities, and are here strengthened by a calcareous plate or plates; but, in *Echinocidaris* and some other *Echinoida*, the pedicels of the oral portion of the ambulacra only, have this structure, while those of the apical portion are pectinated, flattened, and gill-like. Again, in the heterogeneous ambulacra of the *Clypeastroida* and *Spatangoida*, the forms of the pedicels vary much. Thus Müller distinguishes four kinds of pedicels in the *Spatangoida*—simple and locomotive pedicels, without any sucking-disk; locomotive pedicels, provided with terminal suckers, and containing a skeleton; tactile pedicels, with papillose expanded extremities; and gill-like pedicels, triangular, flattened, more or less pectinated lamellæ. Two or three of these kinds of feet may occur in any given ambulacrum, and those which lie within a semita are always different from the others.

In the *Clypeastroida*, the petaloid portions of the ambulacra possess branchial pedicels, interspersed with delicate locomotive pedicels, provided with a calcareous skeleton and with a terminal sucker. The latter kind alone extend on to the oral portions of the ambulacra.

The circumoral nerve of *Echinus* surrounds the œsophagus near the mouth. It has a pentagonal form, and is enclosed by the alveoli, between which the ambulacral nerves pass, over the peristome and through the arches of

the auriculæ, to the ambulacra. Each ambulacral nerve is accompanied by a neural canal, which however ensheathes the nerve, and does not merely lie on its inner side.*

The only known organs of sense in the *Echinidea* are the pigmented "eye-spots," developed in connection with the ends of the ambulacral nerves.

The peritoneal space is filled by a corpusculated fluid, which is kept constantly in motion by cilia distributed over the parietes and the contained viscera. The aeration of this fluid appears to be facilitated in all the *Echinoida*, except *Cidaris*, by five pairs of special branchial plumes developed from the peristome; while, in the *Clypeastroida* and *Spatangoida*, which possess the modified pedicels commonly termed ambulacral gills, there are no such organs.

In the *Echinidea*, a circular pseud-hæmal vessel, whence branches are given off to the genitalia, is said to surround the anus. The alimentary canal is accompanied by two vessels, one on the side of the mesentery (dorsal), the other on the free side (ventral), which communicate with a lacunar network in its walls; and besides these, a fusiform body running parallel with the madreporic canal, and terminating inferiorly in a circular vessel which lies close to the circular ambulacral vessel, around the œsophagus, has been described as a 'heart.'†

The genital organs are sacculated glands, which attain a large size in the breeding season, and open externally by the pores on the genital plates, through which their products are extruded. Hoffmann has found the peritoneal fluid of the males full of spermatozoa.

In the *Echinidea*, as in the *Ophiuridea*, the Echinopædium is a *Pluteus*, and has a skeleton formed of calcareous rods,

* Teuscher, l. c

† According to Hoffmann's latest investigations, there is neither anal nor œsophageal circular vessel in *Spatangus* and *Echinus*. In the former a distinct anastomotic trunk connects the intestinal vessels with the circular ambulacral vessel. In the latter, both intestinal vessels open directly into the circular ambulacral vessel, and what has been described as a heart is really the madreporic canal ("Ueber das Blutgefäss-system der Echiniden," 'Niederlandisches Archiv, Bd. i.).

Fig. 145.

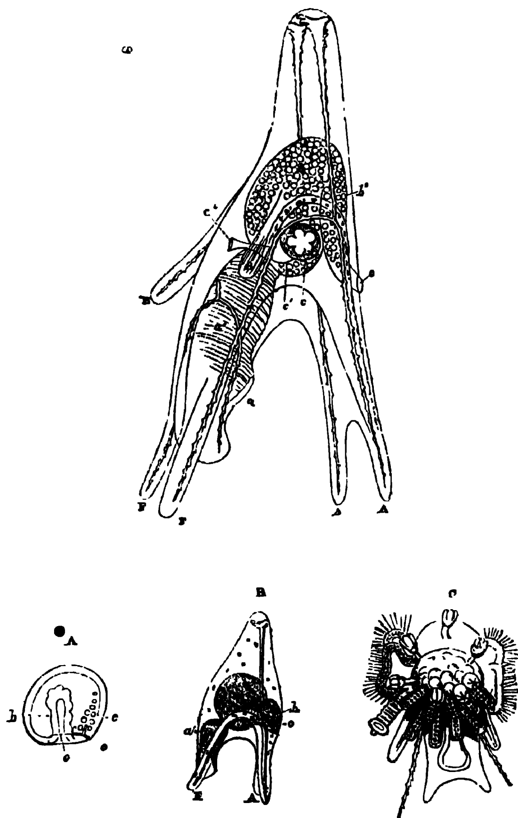


Fig. 145.—Development of an *Echinid.* (After Müller.)—A. Echinopædium of *Echinus pulchellus* in the gastrula stage. B. Fully developed Echinopædium (*Pluteus*) of the same species; *a*, mouth; *b*, stomach and intestine; *c*, anus; A F, processes of the body into which prolongations of the internal skeleton extend. C. The Echinopædium of an Echinid in which the Echinoderm is so far advanced that the spines, pedicels, and pedicellariæ are visible. D.

Echinopædium of *Echinus lividus*: *a*, mouth; *a'* gullet; *b*, stomach; *b'*, intestine; *c*, rudimentary Echinoderm; *c'*, the ambulacral sac; *c''*, the external opening of its duct; *a a*, *f f*, B, the processes of the body.

which support the processes into which the body, in the region of the ciliated bands and elsewhere, is prolonged.

The origin of the ambulacral system, before it has the form of a cæcum with a dorsal pore, has not been made out. The blind end of this cæcum lies on the left side of the alimentary canal, and is connected with a discoidal body, which is situated on the left side of the stomach; a similar body appears on the right side. Doubtless these discoidal bodies answer to the peritoneal diverticula of the alimentary canal of the Echinopædium in other Echinoderms.

The blind end of the tube enlarges, and gives rise to a rosette, whence the ambulacral vessels proceed; and a depression of the integument of the larva, forming the so-called *umbo*, extends inwards to this. At the bottom of the umbo, a new mouth opens through the centre of the rosette into the gastric cavity of the larva, the primitive œsophagus being abolished. The larval skeleton undergoes resorption, but the rest of the Echinopædium passes into the Echinoderm.*

Lovén has recently drawn attention to the fact that, in young Echinids,† the plates of the apical region are not only more conspicuous in relation to the corona, but differ somewhat in their arrangement, from those of the adult. Thus the anus is at first wanting, and the anal plate, which occupies the centre of the apical area, is relatively large; it is united by its edges with the five plates, which, imperforate in the young, will become the genital plates in the adult. The five ocular plates are also imperforate, and

* See, in addition to the memoirs of Müller and Metschnikoff already cited, A. Agassiz, "On the Embryology of Echinoderms." ('Mem. American Academy of Sciences.' 1864.)

† The admirable monograph of A. Agassiz, 'Revision of the Echini,' published in the 'Illustrated Catalogue of the Museum of Comparative Zoology at Harvard College,' is also full of information respecting the young states of the Echinids.

are disposed in a circle outside that formed by the genital plates, their inter-spaces being occupied by interambulacral plates. The apical region of an Echinid has thus, as Lovén points out, a most striking resemblance to the calyx of a Crinoid; the anal plate representing the *basalia*; the genital plates, the *parabasalia*; and the ocular plates, the first *radialia*.

The CRINOIDEA. — This remarkable group, which abounded in former periods of the world's history, is represented at the present day only by the genera *Antedon* (*Comatula*), *Actinometra, Comaster, Pentacrinus, Rhizocrinus* and *Holopus*.

The first three genera are capable of locomotion, while the next two are attached by long articulated stems to submarine bodies. *Holopus*, which is but imperfectly known, appears to be fixed by a short thick unjointed prolongation of its base.

Rhizocrinus lofotensis (Fig. 146), which has been very carefully and elaborately described by Sars,* is a small animal which does not attain more than three inches in length, and lives at great depths (100–300 fathoms or more) in the sea. It consists of a relatively long, many-jointed stem, from many of the articulations of which, branched, root-like filaments, or *cirri*, are given off; at the summit of this is seated a cup-shaped body, the *calyx*, from the margins of which 5-7 arms (*brachia*) radiate. To each arm is attached a double series of alternating *pinnulæ*. The mouth is situated in the centre of that part of the perisoma which forms the surface of the calyx opposite to the stem. The oral aperture is circular, but five (or sometimes only four) triangular lobes of the perisoma, with rounded free ends, project over it, and, when shut, close it like so many valves. From the intervals between these *oral valves* five (rarely four) grooves traverse the oral surface of the calyx, and extend thence throughout the whole length of each arm, giving offsets as they go to the pinnules. Thus the

* 'Mémoires pour servir à la connaissance des Crinoïdes vivants,' 1868.

oral surface of each arm and of each pinnule is deeply excavated.

Between the circular lip and the oral valves, soft flexible tentaculiform pedicels are attached in a single series. Two pairs of pedicels correspond to every valve, each pair arising opposite the basal angle of a valve. These pedicels are hollow, their surface is papillose, and the outer or radial pedicel of each pair is very contractile. Pedicels of the

Fig. 146.

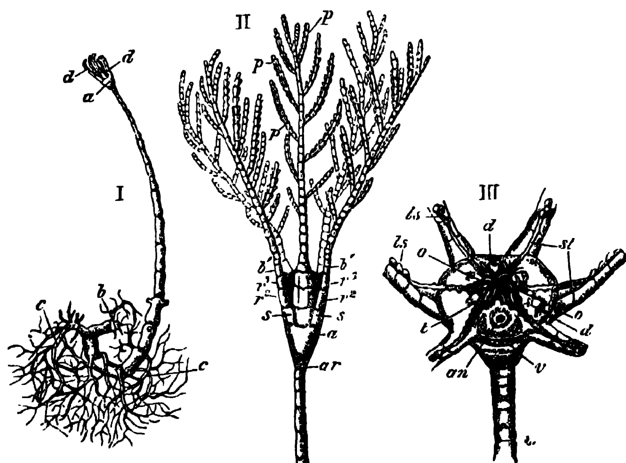


Fig. 146.—*Rhizocrinus lofotensis.* (After Sars.)
I. *Rhizocrinus* entire; *a*, enlarged upper joint of the stem; *b*, larval joints of the stem; *c*, cirri; *d*, brachia.
II. Calyx and arms, with the summit of the stem of a *Rhizocrinus* having five well-developed brachia; *a*, as before; *s*, first radials; r^2, r^3, second and third radials; *b'*, first brachial; *p*, *p*, pinnules.
III. Upper part of the stem and oral face of the calyx, viewed obliquely; *v*, lower part of visceral mass; *s*, *t*, tentacular grooves; *o*, oral valves; *t*, oral tentacles; *an*, anus.

same general character are continued throughout the brachial and pinnular grooves.

The anus is situated at the end of a conical prominence

between two of the grooves on the oral face of the calyx, and is therefore *interradial* in position (Fig. 146, III. *an*).

The skeleton consists of very numerous pieces resulting from the calcification of the perisoma. In the stem they have the form of elongated, subcylindrical, or hourglass-shaped, joints (*articuli*), the opposed faces of which are united by strong elastic ligamentous fibres. The centre of each is traversed by a longitudinal *axial canal*, which extends through the whole length of the stem and is occupied by a soft but solid substance. The distal joint of the stem is not directly fixed to the surface to which the Crinoid is attached, but is connected therewith by the branched *cirri* which proceed from it. Each cirrus has a skeleton composed of joints or *articuli*, somewhat like those of the stem and traversed by a prolongation of the axial canal. Similar cirri are developed from a larger or smaller number of the articuli of the distal portion of the stem.

The proximal joints become gradually shorter in proportion to their length, until they assume a discoidal form. It appears that new articuli are continually added at that end of the stem which lies nearest the calyx.

The summit of the stem, or the base of the calyx, is formed by an enlarged, solid, pear-shaped ossicle, which is probably formed by the coalescence of several *articuli*. Upon this follow five pieces (first *radialia*) closely united together and with a central piece, which probably represents the *basalia* of other Crinoids. The first radial corresponds in direction with the origin of one of the arms, and is followed by a second and third radial. With the third radial is articulated the first of the *brachial* ossicles, which constitute the skeletal support of the unbranched *brachia*. The pinnules are also supported by a series of elongated calcified joints, the basal joint being articulated with a brachial ossicle and the distal joint pointed.

The axial canal dilates in the enlarged pyriform ossicle above-mentioned; and, from the dilatation, branches, which traverse the radial and the pinnular ossicles, are given off. There is a calcareous plate in the substance of each oral

valve, and minute reticulated calcifications are scattered through the perisoma of the oral face of the disk.

The sides of the radial grooves are provided throughout with a double series of oval calcareous plates—the *marginal lamellæ*—which are disposed transversely to the groove, those of opposite sides alternating with one another. They can be erected or depressed; and, in the latter case, overlap one another like tiles.

In *Pentacrinus*, the long stem is fixed by its distal end, and the pentagonal *articuli* of its skeleton give off, at intervals, whorls of unbranched cirri. No distinct basal piece is known, but the calyx appears to begin with the five first radialia. At the third *radiale*, the series bifurcates into two series of *brachialia*, and these again bifurcate to give rise to the *palmaria*, which support the free arms. There are marginal lamellæ along the sides of the tentacular grooves, and a longitudinal series of calcareous ossicles occupies the floor of each groove. The anus is situated upon an elevated interradial cone.

The body of an adult *Comatula* (*Antedon*) answers to the calyx, with its brachia, in other Crinoids.

The centre of the skeleton is constituted by a large *centro-dorsal* ossicle, articulated with the aboral face of which are the numerous cirri, by which the *Antedon* ordinarily grasps the bodies to which it adheres, though it is able, on occasion, to swim freely about. This centro-dorsal ossicle appears to be the homologue of the uppermost part of the stem in the *Pentacrinus*. There are five divergent series of *radialia*, each containing three ossicles. The first radials, or those nearest the centro-dorsal plate, are closely adherent to one another and to the centro-dorsal plate, and are not visible on the outer surface of the calyx. The space left between the apices of the five first radials is occupied by a single plate, the *rosette*,* which is formed by the coalescence of the five *basalia* present in the larva.

The anatomy of the soft parts of the *Crinoidea* has

* Carpenter, 'On the Structure, Physiology, and Development of *Comatula*.' (Phil. Trans. 1866.)

been most thoroughly investigated in the genus *Comatula* (*Antedon*).*

The mouth leads, by a short, wide gullet, into a spacious sacculated alimentary canal, which is coiled upon itself in such a manner as to make about one turn and a half around the axis of the body; and then terminates in the projecting rectal cone which, as has already been seen, is situated interradially, on the oral face of the calyx. The central cavity, included by the coil of the alimentary canal, is occupied by a sort of core of connective tissue, and has received the name of *columella*, but it must be understood that it is not a distinct structure. Bands of connective tissue connect the outer periphery of the alimentary canal with the perisoma.

The five triangular lobes of the perisoma, which surround the mouth like so many valves, contain no calcareous skeleton in the adult *Antedon*. Within these lobes, attached to the oral membrane, there is a circle of tentacula. From the interval between each pair of oral valves, a groove radiates outwards over the surface of the calycine perisoma and speedily bifurcates; one branch goes to the oral surface of each of the arms and runs along it to its extremity, giving off alternate lateral branches to the pinnules in its course.

These grooves are the ambulacral grooves. Their sides are, as it were, fenced by small lobed processes of the perisoma; and, on the inner sides of these processes, groups of minute pedicels take their origin from the sides of the floor of the groove. A thickened band of the ectoderm occupies the middle of the floor, and so strikingly resembles

* E. Perrier, "Recherches sur l'Anatomie de la *Comatula rosacea*" ('Arch. de Zoologie Expérimentale,' 1873). Semper, "Kurze anatomische Bemerkungen über *Comatula*" ('Würzburg Arbeiten,' 1874). Ludwig, "Zur Anatomie der Crinoideen" ('Zeitschrift für Wiss. Zool.' 1876). Carpenter "On the Structure, Physiology, and Development of Antedon" ('Proc. Royal Society,' 1876). Greef, "Ueber den Bau der Crinoideen" ('Marburg Sitzungsberichte.' 1876). P. H. Carpenter, "Remarks on the Anatomy of the Arms of the Crinoids" ('Journal of Anat. and Physiology,' 1876).

the ambulacral nerve of the Star-fish, that the homology of the two, first asserted by Ludwig,* cannot be doubted. Immediately beneath it runs a small canal, discovered by Dr. Carpenter, and termed by him the *tentacular canal*, which gives off lateral branches to communicate with the cavities of the pedicels. A second much wider canal—the *subtentacular canal*—lies beneath this, and is divided by a longitudinal septum. But the septum is incomplete at intervals, and thus the two canals communicate. A third, still larger, *cœliac canal*, is interposed between the floor of the subtentacular canal and the axial skeleton of the arm.

Where the arm joins the calyx, the tentacular canals run beneath the ambulacral groove to the gullet, around which they are united by a circular canal, from which numerous short diverticula, resembling the *vasa ambulacralia cavi* in the Ophiurids, described by Simrock (*l.c.*), depend. The subtentacular and cœliac canals communicate with channels in the perivisceral tissue, on the oral or the aboral face of the visceral mass; and these channels appear, eventually, to open freely into the cavities by which the columella is traversed.

In the partition between the subtentacular and the cœliac canals there lies a cellular cord, or *rachis*, which can be traced back into a reticulation of similar tissue in the visceral mass. The genital glands, contained in the pinnules, are enlargements of lateral branches of this rachis. But the rachis is apparently only an extension of the mesodermal tissue of the visceral mass, comparable to that in which the genitalia are lodged in the Star-fishes; and the multiplication of the genital glands may be regarded as a further extension of the structure which obtains in *Brisinga*. Thus it would seem that the position of the genital glands in the Crinoids is not so anomalous as it at first appears to be.

The centro-dorsal tubercle contains a cavity, with which the canals which traverse the ossicula of the cirri, the calyx, the brachia and the pinnules communicate. This

* 'Zeitschrift für Wiss. Zool.,' 1876.

cavity was considered by Müller to be a heart. It proves, however, to be largely filled by solid tissue, which is continued not only into all the canals which traverse the ossicula, but also into the columella, or tissue which occupies the centre of the coils of the alimentary canal.

Dr. Carpenter * is of opinion that so much of this axial tissue as occupies the cavity of the central tubercle, and is continued throughout the ossicula of the calyx and arms, is the proper central organ of the nervous system; founding this opinion partly upon the fact that, when this mass is irritated in a living *Antedon*, a sudden contraction of all the muscles of the arms takes place; and partly upon the distribution of the ultimate ramifications of the axial tissue in the arms. Greef, on the contrary,† affirms that all these tracts can be injected, and retains the name of 'heart' for the cavity of the centro-dorsal tubercle.

The perisoma of the oral surface of *Comatula* exhibits a great number of minute circular pores, with thickened cellular margins. Greef has discovered that these are the external apertures of canals, with ciliated walls, which open into the body cavity, and readily allow fluids to pass into, or out of, that cavity.

Each mature ovary of *Antedon* has a distinct aperture, through which the ova are discharged, and to which they adhere for some days like bunches of grapes. The testis developes no special aperture, but the spermatozoa appear to be discharged by dehiscence of the integument.

Since the discovery by Vaughan Thompson that *Comatula* passes through a Pentacrinoid larval condition, the development of the free Crinoids has been the subject of various investigations,‡ and the following results may be regarded as established.

Complete yelk-division takes place. The morula ac-

berichte,' 1876).

‡ See Wyville-Thomson ('Phil.

Metschnikoff
les
g,'
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('Archiv für Mikroskopische Anatomie,' 1876).

quires an oval form, and developes four hoop-like bands of cilia, with a tuft of cilia at the hinder end. Between the third and fourth bands of cilia, counting from the anterior end of the Echinopædium, the blastoderm becomes invaginated, and gives rise to an archenteron. In the interspace between this blind sac, the wall of which is the hypoblast, and the epiblast, constituted by the rest of the blastoderm, a mesoblast composed of reticulated cells makes its appearance. The blastopore closes, while the archenteron detaches itself from its attachment to the posterior ventral face of the larva, and becomes connected with an œsophageal involution formed at its anterior end. The archenteron next throws out three diverticula, of which two are lateral, and one is ventral. The lateral diverticula enlarge, and apply themselves to the rest of the archenteron, now become the intestine, from which they are soon completely shut off, and converted into peritoneal sacs. The left sac thus formed lies on the ventral side of the intestine, the right sac on its dorsal side. The walls of the two sacs become applied together, and form a circular mesentery. The peritoneal sac of the aboral side sends a process into the hinder end of the body, which has begun to elongate, in order to give rise to the stem of the Pentacrinoid form.

The third, or ventral, diverticulum is shut off from the alimentary canal much later than the other two. It grows round the mouth, and gives rise to the circular ambulacral vessel, whence the tentacular canals are given off.

Ten plates, each consisting of a calcareous network and arranged in two rows of five each, next appear in the substance of the Echinopædium around the alimentary canal. From the centre of the posterior row, eight calcareous rings extend through the length of the body of the larva, enclosing the backward prolongation of the aboral peritoneal sac; and the series terminates by a broad discoidal network which lies on one side of the posterior end of the larva. This discoidal plate is that which occupies the attached end of the stem of the future Crinoid; the rings become the *stem*, and the two circles of plates the basal

and oral ossicula of the calyx, respectively. As the stem elongates, new rings (*articuli*) are added at the junction of the stem with the calyx.

The larva now fixes itself by the discoidal end of its stalk, which becomes relatively longer and narrower; while the part of the body which contains the basal and oral plates, and is to be converted into the calyx, remains thick and short. Its broad end becomes five-lobed, each lobe answering to an oral plate. These plates separate like the petals of a flower bud, and discover, in the centre, the wide permanent oral aperture. Between the margins of this and the oral plates, tentaculiform pedicels, at first only five, but eventually arranged in groups of three, between every pair of oral plates, make their appearance.

The alimentary cavity is still a mere sac, without intestine or anus.

Five radial plates next appear in the wall of the calyx between the basal and the oral plates, and alternating with both; and, in correspondence with them, the arms grow out as rapidly elongating processes, in which the other radials are successively developed. The entire zone of the calyx, which is occupied by the origins of the arms, at the same time widens, so that the oral plates, which remain round the mouth, and the basal plates, which encircle the stem, become widely separated. The intestine grows out as a diverticulum of the alimentary cavity and opens on an interradial elevation of the calyx, in which an anal plate is developed. The young Echinoderm has now passed into the stalked Pentacrinoid stage.

In *Comatula*, the oral and anal plates disappear altogether, and the basals coalescing into the rosette, are hidden by the first radials, on the one hand, and the centro-dorsal tubercle, which represents coalesced joints of the stem, on the other. The arms bifurcate and acquire their pinnules; and the calyx, with its appendages, eventually becomes detached from its stem as a free *Comatula*. In the existing stalked Crinoids, such as *Pentacrinus*, on the other hand, the segments of the stem acquire whorls of cirri, at

intervals, and no such modification of the uppermost segments into a centro-dorsal tubercle takes place.

On comparing the facts of structure and development which have now been ascertained in the five existing groups of the *Echinodermata*, it is obvious that they are modifications of one fundamental plan. The segmented vitellus gives rise to a ciliated morula, and this, by a process of invagination, is converted into a gastrula, the blastopore of which usually becomes the anus. A mouth and gullet are added, as new formations, by invagination of the epiblast. The embryo normally becomes a free Echinopædium, which has a complete alimentary canal, and is bilaterally symmetrical. The cilia of its ectoderm dispose themselves in one or more bands, which surround the body; and, while retaining a bilateral symmetry, become variously modified. In the *Holothuridea*, *Asteridea*, and *Crinoidea*, the larva is vermiform, and has no skeleton; in the *Echinidea* and the *Ophiuridea* it becomes pluteiform, and developes a special spicular skeleton.

If an Echinopædium were to attain reproductive organs, and reproduce its kind, I think that it cannot be doubted that its nearest allies would be found among the *Turbellaria*, the *Rotifera*, the *Gephyrea* and the *Enteropneusta*.* But that which characterises the *Echinodermata* is the fact that the alimentary canal of the Echinopædium gives rise to an enterocœle, which again is subdivided into two

* In a report upon the 'Researches of Prof. Müller into the anatomy and development of the Echinoderms,' published in the 'Annals of Natural History' for July 1851, I drew attention to the affinities of the Echinoderms with the Worms; and in a paper on *Lacinularia socialis*, read before the Microscopical Society in the same year, I expressed the view that the *Rotifera* 'are the permanent forms of Echinoderm larvæ, and hold the same relation to the Echinoderms, that the Hydriform Polypi hold to the Medusæ,' and that they 'connect the Echinoderms with the Nematidæ and the Nematoid Worms.' When they were published, those who did not ignore these views, ridiculed them. Nevertheless, though somewhat crudely expressed, I think it will be admitted they have been substantially justified by the progress of knowledge during the last quarter of a century.

systems of cavities, one ambulacral and the other peritoneal, and that the mesoblast becomes modified in accordance with the arrangement of these systems. The enterocœle may be formed by one diverticulum or by three? In the former case, the first formed becomes subdivided into three, of which one is anterior, and two lateral, as in the latter case. The lateral diverticula give rise to the peritoneal cavity and its lining: the median diverticulum is converted into the circular ambulacral vessel and its dependencies; and it is in consequence of the radiating disposition of the latter, and of the nerves and muscles which are related to it, that the Echinoderm possesses so much radial symmetry as it displays. It is clear, therefore, that the radial symmetry of the Echinoderm results from the secondary modification of an animal, which is primitively bilaterally symmetrical; and that the apparently radiate *Echinus* or Star-fish is a specially modified 'Worm,' (using that term in its widest sense) in the same sense as the apparently radiate *Coronula* is a modified Arthropod.

Haeckel goes further than this, and supposes that each ray of a Star-fish or Ophiurid, for example, represents a Worm, and that the Echinoderm consists of coalesced vermiform buds, developed in the interior of the Echinopædium. I must confess my inability to see that this hypothesis is supported by valid reasons. On the contrary, the more closely one compares the structure of the ray of an Echinoderm with the body of any known Annelid, the more difficult does it appear to me to be to find any real likeness between the two.

In order to find any analogy for the production of the Echinoderm within the Echinopædium, on the contrary, it appears to me that we must look to the lower and not to the higher morphological types. Among the *Hydrozoa*, nothing is commoner than the distribution of the functions of life between two distinct zooids, one of which alone developes reproductive organs. In the former, the *hydranth*, radial symmetry is often hardly discernible (*e.g. Calycophoridæ*); in the latter, the *medusoid*, it is very marked,

and especially characterises the arrangement of the gastro-vascular canals; which are offshoots of the alimentary cavity, and if they became shut off therefrom, would answer to the enterocœle of the Echinoderm.

Suppose that from a hydranth such as that of a *Diphyes*, a medusoid were developed, and that instead of projecting from the exterior of the body, it remained hypodermic, spreading out between the ectoderm and the endoderm of the hydroid, and consequently superinducing a very marked radial symmetry upon it. The resulting form would give us a Cœlenterate which would be a close analogue of an Echinoderm.

In a certain sense, an Actinozoon may be fairly regarded as such a combination of a hydroid with its medusoid; and, hence, it must be conceded that the parallel between the gastro-vascular system of the *Ctenophora* and the ambulacral system of the Echinoderms, instituted by the elder Agassiz, was well worthy of consideration. Shut off the gastro-vascular canals of a Cydippe from the alimentary canal, and they become an enterocœle, of which the prolongations along the stomach may be compared with the peritoneal sacs, and those beneath the paddles with the ambulacral vessels of the Echinoderm.

But there is a long step between the admission of the force of these analogies, and the conclusion that the Echinoderms and the *Cœlenterata* are so closely allied as to be properly associated in one natural assemblage of "Radiate" animals. On the contrary, the Echinoderm, by its Echinopædium stage, shows an advance in organisation, far beyond anything known in the *Cœlenterata*; and in the highly characteristic mode of development of its enterocœle (the elucidation of which in the Star-fishes by Prof. A. Agassiz, is the most important advance in our knowledge of the Echinoderms made since the time of Müller), the Echinoderm agrees with the higher, and not with the lower *Metazoa*.

Echinodermata abound in the fossil state. Calcareous

plates, referred to the *Holothuridea*, occur in the mesozoic rocks, but are not known earlier. The Star-fishes are met with in the older Palæozoic strata, under forms very similar to some of those which now exist. The *Echinidea* abound from the Upper Silurian (*Palæchinus*) onwards. The Palæozoic forms are spherical, and have multiple interambulacral plates and simple ambulacra. *Echinidea* of the modern type appear in the Mesozoic strata, the *Echinoida* first; while the *Spatangoida* and *Clypeastroida* are of later date. This order of occurrence agrees with the embryonic development of the two latter groups, which are more nearly spherical when young than subsequently.

The *Crinoidea* abound in the Palæozoic and older Mesozoic rocks, gradually diminishing in number in later formations. The oldest appear to have all been stalked, and of peculiar and extinct types.

Three groups are wholly extinct, and are unknown in strata newer than the Carboniferous formation. These are the *Cystidea*, the *Edrioasterida*, and the *Blastoidea*.

The CYSTIDEA.—In their general characters the *Cystidea* come very near the Crinoids. *Cryptocrinus*, the simplest form of the group, possesses a calyx supported on a stem, and composed of five *basalia*, five *parabasalia*, and five *radialia*. An inter-radial aperture is surrounded by a cone of small plates, termed the *pyramid*. The antambulacral surface has no pores, but these were present in other genera, and sometimes are scattered irregularly (*Caryocrinus*); sometimes disposed in pairs (*Sphæronites*); while sometimes they take the form of parallel slits arranged in "pectinated rhombs." The arms were free (*Comarocystites*), or recurved and closely applied to the calyx. They bore pinnules, which, in consequence of the non-development of the arms, were sometimes sessile on the radialia. In the species with recurved arms, the latter simulate calycine ambulacra. There is an aperture placed in the centre of the calyx at the point of convergence of the ambulacra; another small one on one side of this; and, thirdly, the aperture of the pyramid. The first of

these is commonly regarded as the mouth, the second as the anus, the third as the reproductive aperture.

The *Cystidea* would, on this interpretation, differ from all other *Echinodermata*, except the *Edrioasterida* and *Holothuridea*, in the genital outlet being single; but around the central aperture five pores are seen, in some species at least, to which a genital function has been ascribed. In any case, the *Cystidea* would appear to come very close to the *Crinoidea*.

The EDRIOASTERIDA.—This group contains several genera of extinct Echinoderms (*Edrioaster*, *Agelacrinites*, *Hemicystites*), which, in general form, somewhat resemble what the Asterid *Goniaster* would be if its angles were rounded off. Like the *Cystidea*, they possess an interambulacral *pyramid*, but they differ from them in that they have ambulacra perforated by canals which open directly into the cavity of the calyx, and that they possess no arms. The *Edrioasterida* have no stem, but seem to have been attached by the aboral face of the body.

The BLASTOIDEA.—In *Pentremites*, the representative of this order, the ambulacral and antambulacral regions are nearly on an equality: the body is prismatic or subcylindrical. The pedunculated calyx is composed of three basal plates, two of which are double. The aboral plates receive in their intervals five plates deeply cleft above. In the clefts lie the apices of the ambulacra, the oral portions of which are included between the five deltoid inter-radial pieces which surround the mouth. The cleft plates are not radials, but portions of the perisomatic skeleton of the aboral region. Surrounding the central, probably oral, aperture are four double pores, and a fifth divided into three. The median of these three seems to be anal, the others and the paired pores being genital. Each ambulacrum is lanceolate in form, and presents superficially a double row of ossicles, which meet in the middle line and support pinnules at their outer extremities; beneath them lies a single plate, perhaps the homologue of the vertebral ossicles in the *Ophiuridea*: beneath it again are parallel canals, the nature of which is unknown.

CHAPTER X.

THE TUNICATA OR ASCIDIOIDA.

THIS remarkable and, in many respects, isolated group of marine animals contains both simple and composite, fixed and free organisms. None attain a length of more than a few inches, and some are minute and almost microscopic.

The simplest members of the group, and those the structure of which is most readily comprehensible are the *Appendiculariæ;* minute pelagic organisms, which are found in all latitudes, and are propelled like tadpoles, by the flapping of a long caudal appendage at the surface of the sea.

Appendicularia flabellum (Fig. 147) has an ovoid or flask-shaped body (A), one-sixth to one-fourth of an inch in length. The appendage (B) is from three to four times as long as the body, to one face of which it is attached near, but not at, the posterior extremity. It is flattened, and is supported by a firm central axis, which may be termed the *urochord* (Fig. 147, a). The greater part of the body is usually invested by a structureless gelatinous substance, but, on its rounded hinder extremity, this ceases to be distinguishable from the ectoderm.

On the caudal appendage the polygonal contours of the cells of which the ectoderm is composed, are plainly discernible.

The mouth has an overhanging lip. It leads into a large pharyngeal sac, the walls of which are formed by the endoderm. Posteriorly, this sac narrows into the œsophagus, which bends towards the hæmal side of the body, and then opens into a spacious stomach, which takes a transverse direction and is divided into two lobes, a right and a left.

From the left lobe, the intestine arises; and, bending inwards, turns abruptly forwards in the middle line, where it terminates midway between the oral aperture and the attachment of the caudal appendage. The intestine there-

Fig. 147.

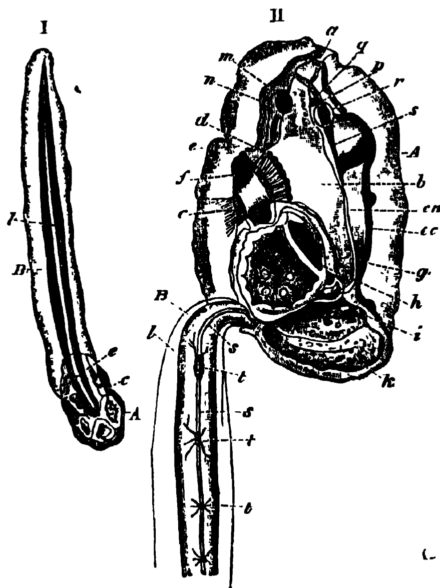


Fig. 147.—*Appendicularia flabellum*.
I.—The entire animal with the caudal appendage in its ordinary position, or turned forwards.
II.—Side view of the body, with the caudal appendage forcibly bent backwards.
A, the body; B, the caudal appendage; *a*, oral aperture; *b*, the pharynx; *c*, an atrial opening; *d*, the corresponding stigma, with its cilia; *e*, anus; *f*, rectum; *g*, œsophagus; *h*, *i*, stomach; *k*, testis; *l*, urochord; *m*, cellular patch at the side of the oral end of the body; *n*, endostyle; *p*, ganglion; *q*, ciliated sac; *r*, otocyst; *s*, posterior nerve with its ganglia, *t*; *en*, endoderm; *e c*, ectoderm.

fore has a hæmal flexure. In the middle of its hæmal aspect the endoderm of the pharyngeal cavity is raised into

a fold, which projects into the blood cavity contained between the endoderm and ectoderm. The walls of the bottom of the fold are thicker than the rest, so that, viewed sideways, it has the aspect of a hollow cylinder. This is the *endostyle.** (Fig. 147, *n.*)

The endoderm of the pharynx is ciliated, and the cilia are especially large over a narrow tract, or *peripharyngeal band*, which encircles the oral aperture at the level of the anterior end of the endostyle, and is continued back, as a *hypopharyngeal band*, along the middle of the neural face of the pharynx to the œsophageal opening.

On each side of the endostyle, the posterior part of the hæmal wall of the pharynx presents two oval apertures or *stigmata* (Fig. 147 *d*), encircled by cells, which are provided with very long and active cilia. Each stigma leads into a funnel-shaped *atrial canal*, the open end of which terminates beside the rectum.† (Fig. 147, *c.*)

The heart is a large sac, which exhibits rapid peristaltic contractions, and is placed transversely between the two lobes of the stomach. In the species which I observed no blood corpuscles could be seen, and the direction of the pulsations of the heart was not reversed at intervals, as

* So described and named in my "Observations upon the Anatomy and Physiology of Salpa and Pyrosoma, together with remarks upon Doliolum and Appendicularia." (Phil. Trans. 1851.) In 1856, however, I stated "With regard to the endostyle, I have nothing important to add to my previous account, except that I believe it to be here, as in other ascidians, the optical expression of the thickened bottom of a fold or groove of the branchial sac." ('Quarterly Journal of Microscopical Science,' April, 1856.) In my memoir on Pyrosoma (Linn. Trans. 1860, p. 205) the endostyle is stated to be "in reality a longitudinal fold or diverticulum of the middle of the hæmal wall of the pharynx, which projects as a vertical ridge into the hæmal sinus, but remains in free communication with the pharynx by a cleft upon its neural side."

† These stigmata were first described by Gegenbaur ("Bemerkungen über die Organization der Appendicularien;" Zeitschrift für Wiss. Zoologie, 1855), who supposed that they communicated with canals of the interior of the body. However, by feeding *Appendicularia* with indigo, I demonstrated the communication of these stigmatic funnels with the exterior of the body. ('Quarterly Journal of Microscopical Science,' l.c.)

it is in the Ascidians in general. M. Fol,* however, states that, in other *Appendicularia*, the reversal of the contractions of the heart takes place. Like myself he has been unable to discover any blood corpuscles. There are no distinct vessels, but the colourless fluid which takes the place of blood makes its way through the interspaces between the ectoderm and endoderm and the various viscera.

The nervous system consists of a ganglion (Fig. 147, *p*) situated nearly opposite the anterior end of the endostyle; in front, this gives off the nerves to the sides of the mouth, while, behind, it is continued into a long cord (*s*), which runs back beside the œsophagus, and between the lobes of the stomach, to the base of the appendage. It then passes along one side of the urochord to its extremity, giving off nerves at intervals. At the origins of these nerves aggregations of ganglionic cells are situated (Fig. 147, *t*). The most anterior of these ganglia is the largest.†

A rounded otocyst containing a spherical otolith is attached to the ganglion, and a small ciliated sac, which opens into the pharynx, is in close relation with it (Fig. 147, *r*, *q*). M. Fol describes a number of fine tactile setæ situated around the oral aperture.

The urochord, which constitutes the axial skeleton of the appendage, is transparent, rounded at each end, and bounded by a delicate membrane. The remains of the cells of which it is composed are to be seen in it, here and there, as ramified corpuscles lodged in its periphery.

The only muscles hitherto observed in *Appendicularia* are two sheets of striped fibres interposed between the urochord and the cellular ectoderm of the appendage.

The reproductive organs occupy the rounded projection formed by the posterior part of the body behind the

* 'Etudes sur les Appendiculaires,' 1872.

† 'Quarterly Journal of Microscopical Science,' 1856, pp. 8, 9. M. Fol, who finds the same arrangement in other *Appendicularia*, counts this as the second ganglion of the nervous system, and states that a fine canal traverses both the ganglia and the longitudinal nerve.

digestive canal. The testis (Fig. 147, *k*) is a large cellular mass which fills the greater part of the cavity of this projection in the adult. When fully formed, it is resolved into spermatozoa with rod-like heads about $\frac{1}{7000}$th of an inch long and very fine filiform tails. They escape by the dehiscence of the testis.

I have never met with *Appendiculariæ* containing ova, nor do any other observers, except M. Fol, appear to have been more fortunate. The latter, however, states that these animals are hermaphrodite (*Oikopleura dioica* apparently is diœcious), and that the ovary is developed later than the testis.*

Two singular rounded patches of a cellular structure (Fig. 147, II. *m*) are interposed between the ectoderm and the endoderm on each side of the anterior end of the endostyle. Similar bodies occur in other Ascidians, but their function is unknown.

One of the strangest peculiarities of the *Appendiculariæ* is the power which they possess of excreting from the surface of the ectoderm, with extreme rapidity, a mucilaginous cuticular investment, in the interior of which, as in a spacious case, the whole body is lodged. This is what was originally described by Mertens as the "house" of the *Appendicularia*. It is obviously the homologue of the test of other Ascidians, which is often adherent to the ectoderm by only two or three points; but no cellulose has been discovered in it. According to M. Fol, who has studied the formation of the "house" with great care, the *Appendiculariæ* have no proper test, and what I have described as the structureless gelatinous investment of the anterior part of the body is the commencement of the "house." It increases, assumes a peculiar

* I must confess that M. Fol's figures and descriptions of the ovary and ova are not satisfactory to me, and his dismissal of the subject of their development in the following paragraph is tantalising:—

"Le développement, que j'ai pu suivre jusqu'à la formation de la larve, ne me parut différer en rien de celui des Ascidies; et comme d'autre part, la petitesse de ces œufs et la difficulté qu'on a de les obtenir les rendent peu favorables à l'étude, je n'ai pas jugé à propos d'approfondir davantage ce sujet." (l. c. p. 1.)

fibrous structure, and in the course of an hour, in a vigorous animal, it is separated as an envelope in which the whole body is capable of free movement. In front, it presents two funnel-shaped apertures supported by a fibrous trellis-work, which lead down to the cavity in which the body is contained. A spacious median chamber allows of the free motion of the tail. After a few hours the animal deserts its test and forms another.

In the great majority of those *Tunicata* which are fixed in the adult state, the young leave the egg in an active larval condition, and resemble *Appendicularia* in being propelled by a muscular appendage in the axis of which lies an urochord. The body and appendage, however, are invested by a coat, or *test*, impregnated with cellulose, and the former presents some important structural differences from that of *Appendicularia*. After a free existence of a certain duration, the body of the larva fixes itself, the appendage withers away, and the young animal assumes the ordinary form of a fixed Ascidian. It may remain simple, or it may develope buds and give rise to a compound organism or *Ascidiarium*, consisting of many Ascidiozooids united together.

All the fixed Tunicates present two, more or less closely approximated, apertures; one, *oral*, leads into the alimentary cavity, the other, *atrial*, opens into a chamber, the *atrium*, into which the fæces and genital products are poured. During life, when these apertures are open, a current sets into the oral and out of the atrial opening. But if the animal is irritated, the sudden contraction of the muscular walls of its body causes the water contained in the brachial and atrial cavities to squirt out in two jets, while both apertures are speedily closed.

The apertures are much further apart in some forms than in others, and in certain of the *Botryllidæ* they are almost terminal. In the pelagic genera *Pyrosoma* (Fig. 150), *Doliolum* (Fig. 151), and *Salpa* (Fig. 152), the atrial and oral apertures are at opposite ends of the longest diameter of

the body; and, in the two latter, locomotion is effected by the contraction of transverse muscular bands, which drives

Fig. 148.

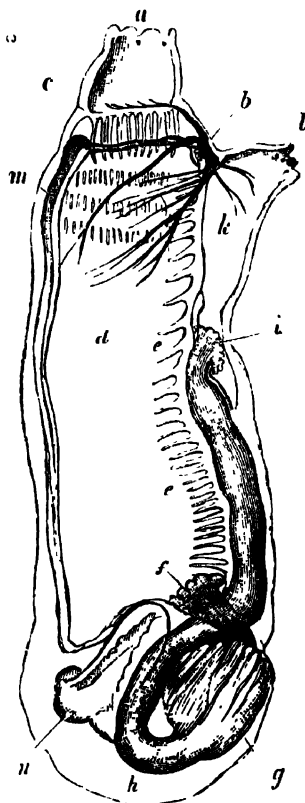


Fig. 148.—*Phallusia mentula.*—The test is removed, and hardly more of the animal represented than would be seen in a longitudinal section: *a*, oral aperture; *b*, ganglion; *c*, circlet of tentacles; *d*, branchial sac, the three rows of apertures in its upper part indicate but do not represent the stigmata; *e*, the languets; *f*, the œsophageal opening; *g*, the stomach; *h*, the intestine; *i*, the anus; *k*, the atrium; *l*, the atrial aperture; *m*, the endostyle; *n*, the heart.

the water out of the one aperture or the other, and causes the body to be propelled in the opposite direction.

When one of the simple fixed Ascidians, such as a *Phallusia* (Fig. 148) or a *Cynthia*, is laid open by a section carried through the oral opening, at right angles to a transverse plane passing through its centre, the mouth is found to open into a large pharyngeal dilatation, termed the *branchial sac* (Fig. 148, *d*). A series of simple or pinnatifid tentacles (Fig. 148, *c*) is seen encircling the oral aperture, at some little distance within the margin of the lip, which is usually divided, like that of the atrial opening, into four or six lobes. Immediately behind the tentacular circlet is a ciliated peripharyngeal band.

On that side of the branchial cavity which is furthest away from the atrial opening, a pair of delicate lip-like folds extend, parallel with one another, from the peripharyngeal band, along the middle line of the branchial sac, as far as the opening of the œsophagus at the opposite end of the branchial sac. The interspace between these leads into a fold of the endoderm, lined by a thick epithelium and forming the endostyle, and, in the middle line of the *peripharyngeal band*, on the same side as the atrial aperture, there is a tubercular elevation, which contains a ciliated cavity and answers to the ciliated sac of *Appendicularia*. The walls of this sac are variously folded, and, consequently, the surface of the tubercle presents a more or less complicated pattern. Continued backwards in the middle line, as far as the œsophageal aperture on this side of the branchial sac, there are sometimes one, sometimes two longitudinal lamellæ, the *hypopharyngeal folds*; or there may be merely a ridge surmounted by a series of tentacles, termed *languets* (Fig. 148, *e*). The languet which is nearest the ciliated sac is often the largest of the series. Behind the peripharyngeal band, the lateral walls of the pharyngeal, or branchial, sac are perforated by small elongated apertures, the *stigmata*, the edges of which are fringed with long cilia; and, by means of these apertures, the cavity of the sac communicates with the atrium.

The stigmata are arranged in transverse rows and are usually very numerous. The reticulated wall of the branchial sac may be strengthened by longitudinal lamellæ, or it may be raised into few and distant, or many and close-set folds. In some cases, papillæ of a complicated form are developed from the inner surface of the sac, and its outer wall is always connected by vascular trabeculæ with the parietal wall of the atrium. In some cases, (*Molgula*) the stigmata, instead of being elongated meshes, are coiled spirally. The atrial chamber (Fig. 148, *k*), into which the branchial stigmata open, is shown by laying it open from the atrial aperture, in the same way as the branchial chamber was laid open from the oral aperture. The atrial opening is thus seen to lead into a cavity, interposed between the branchial sac and the parietes, and lined upon all sides by a delicate membrane (the *third tunic* of Milne-Edwards) like a peritoneum. This membrane has a parietal and a visceral layer. The former is continued from the atrial aperture on to the parietes of the body, to the level of the peripharyngeal band in one direction, to a line parallel with the endostyle in another, and to the alimentary and genital viscera in a third direction. From these various lines, it is reflected on to the branchial sac, of which it forms the outer wall. At the margins of the stigmata it is continuous with the endoderm of the pharynx, and, at the aperture of the rectum, with the endoderm of the intestine. Thus the atrial membrane forms a bilobed sac, one lobe extending on each side of the pharynx, and opens outwards by the atrial aperture; it communicates by the stigmata with the interior of the branchial sac; and, by the anal and genital openings, it receives the fæces and genital products. The current which sets in at the oral and out at the atrial aperture is set in motion by the cilia of the stigmata.

The atrium of the higher Ascidians differs from that of *Appendicularia*, not only in extent, but in being single and not double; and in its single aperture being placed upon the neural aspect of the body close to the ganglion, while the atrial funnels of *Appendicularia* open upon the hæmal

aspect of the body. The development of the higher *Tunicata*, however, shows that the peculiarities of the atrium in them are of secondary origin; and that, to begin with, there are two distinct atria, as in *Appendicularia*.

The œsophageal aperture is usually surrounded by a raised lip, and the short and wide œsophagus leads into a dilated stomach, whence a shorter or longer intestine proceeds. The alimentary canal is always bent upon itself in such a manner that the anus terminates on the neural side of the body, in the atrial chamber.

In *Clavelina*, *Amouroucium*, *Didemnum*, *Syntethys*, and most of the compound Ascidians, the greater part of the alimentary canal lies altogether beyond the branchial sac, in a backward prolongation of the body which has been termed the *abdomen*, and is often longer than all the rest of the body; the alimentary canal forming a long loop, and the direction of the axis of the branchial sac being continued by that of the gullet, stomach, and first half of the intestine. In the *Botryllidæ*, however, the stomach is bent at right angles upon the gullet, as in *Appendicularia*; the intestine almost immediately turns forward, and then, turning sharply upon itself, passes forwards parallel with the hinder part of the branchial sac, on one side of which it opens into the atrium.

A similar arrangement obtains in *Perophora*, but the branchial sac extends backwards for a short distance on one side of the stomach. In the solitary Ascidians, the stomach lies sometimes altogether behind the branchial sac (*Pelonaia*, some *Phallusiæ*); but, usually, the branchial sac extends so far back that the whole alimentary canal lies on one, usually the right, side of it. In *Phallusia monachus*, the hinder end of the branchial sac is recurved, and the œsophageal opening looks backwards to the fundus of the sac, instead of forwards to the mouth.

In many Ascidians, a strong fold of the endoderm of the intestine projects into its interior, as in Lamellibranchs and in the Earthworm, where such a fold constitutes the so-called *typhlosole*.

In the pelagic Tunicates, *Salpa*, *Pyrosoma*, and *Doliolum*, I found a system of fine tubules * which ramify over the intestine and are eventually gathered together into a duct which terminates in the stomach. An apparatus of the same nature exists in *Phallusia*, *Cynthia*, *Molgula*, *Perophora*, *Botryllus*, *Botrylloides*, *Clavelina*, *Aplidum*, and *Didemnum*, † and I have little doubt that it is hepatic in its function. In some *Cynthiæ*, however, there is a follicular liver of the ordinary character, which opens into the stomach by several ducts.

In some *Phallusiæ*, the alimentary canal is coated by a very peculiar tissue, consisting of innumerable spherical sacs containing a yellow concretionary matter. In *Molgula* (and in the *Ascidia vitrea* of Van Beneden) an oval sac containing concretions lies close to the genital gland, on one side of the body. As these concretions have been shown by Kupfer ‡ to contain uric acid, the organ must be regarded as renal in function. M. Lacaze-Duthiers § terms this sac an "organ of Bojanus;" but, as he admits, no opening is discoverable: it would probably be more correct, therefore, to regard it as the representative of the glandular part of the organ of Bojanus. ||

The heart is an elongated sac open at each end, lodged near the stomach, and close to the hinder extremity of the branchial sac. After a certain number of contractions in one direction, it stops and contracts for the same number

* Savigny seems first to have observed this organ, as would appear from his account of *Diazona*, ('Mémoires sur les Animaux sans vertèbres,' p. 176,) and the description of plate 12. Lister mentions and figures it in *Perophora* (Phil. Trans. 1834).

† 'Reports of the British Association,' 1852. Hancock "On the Anatomy and Physiology of the *Tunicata*." ('Journal of the Linnean Society,' Vol. IX.) The development of these tubules from the stomach was traced by Krohn in *Phallusia*, and by myself in *Pyrosoma*.

‡ "Zur Entwickelung der einfachen Ascidien." ('Archiv für Mikr. Anatomie,' 1872.)

§ "Les Ascidies simples des Côtes de France." ('Archives de Zoologie expérimentale,' 1874.) M. Lacaze-Duthiers has obtained murexide by heating this substance with nitric acid.

|| There is a close resemblance between the cells of which this organ is composed and those which constitute the primitive kidney in the *Pulmonata*.

of times, in the opposite direction. The course of the circulation is thus reversed with great regularity. The blood is a clear fluid, containing colourless corpuscles.

Respiration is effected in the walls of the branchial sac through which the blood is driven. The supply of aerated water is kept up by the currents already mentioned, which subserve the ingestion of food, the respiratory process and the ejection of effete matters, as well as the expulsion of the generative products. The test in which the body is enclosed is sometimes closely adherent to the surface of the ectoderm, but sometimes is united with it only at the oral and atrial apertures, and by prolongations of the body. In consistency it presents every variety, from soft and gelatinous, to dense and hard like cartilage, or tough, like fibrous tissue. In some cases the exterior of the test is covered with horny spines, tubercles, or even with regularly disposed plates (*Chelyosoma*).

In texture, the test may present merely a homogeneous matrix, in which cells like connective tissue corpuscles may be scattered; or it may resemble cartilage (*Phallusia*) or fibrous tissue. In most cases it is non-vascular; but, sometimes, tubular prolongations of the ectoderm, divided by a median septum and containing blood, enter it at one point, and thence branch out through its substance.

In the *Chevreulius* of Lacaze-Duthiers,* the test is somewhat like a snuff-box with a moveable lid. There is no hinge, however, but the substance of the lid is continuous with that of the rest of the test along the line of junction. And the elasticity of this part causes the lid to stand open, unless it is shut by the contraction of two adductor muscles which are attached to it.

The reproductive organs of the two sexes are united. Usually, the testis and the ovary have the form of racemose glands situated in the loop formed by the intestine; or beyond it, when the 'abdomen' is long; and their ducts run, parallel with one another, to open close together beside the anus. In many of the simple Ascidians, however, the

* 'Annales des Sciences Naturelles,' 1865.

Fig. 149.

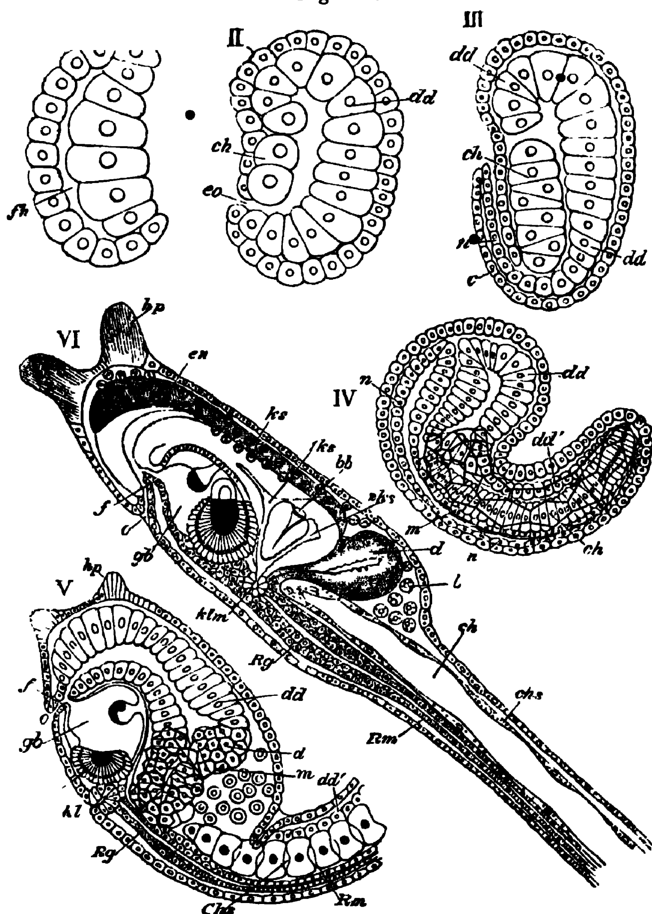


Fig. 149.—*Phallusia mammillata.*—Various stages in the development of the larvæ. (After Kowalewsky.)*

* "Weitere Studien über die Entwickelung der einfachen Ascidien." ('Archiv für Mikr. Anat.', 1871.)

I. The vesicular morula, flattened and about to undergo invagination; *fh*, blastocœle. The large blastomeres constitute the hypoblast, the small ones the epiblast.
II. The gastrula with the blastopore, or opening of invagination, *eo*; *ch*, the blastomeres which constitute the rudiment of the urochord; *dd*, the remaining blastomeres of the hypoblast.
III. A more advanced embryo; *ch*, *dd*, as before. *c*, the epiblast; *n*, the nervous layer of the neural cavity, which is now open only in front near *ch*.
IV. An embryo with the caudal appendage distinct. The nerve tube *n* is complete, and the muscle-cells *m*, are distinguishable.
V. The body of a larva as it escapes from the egg. *a*, the eye; *gb*, the saccular anterior end of the central nervous apparatus into which the otolith projects; *Rg*, *Rm*, its tubular backward prolongation; *Chs*, cells of the urochord; *o*, mouth; *kl*, atrial aperture; *f*, opening at the anterior end of the central nervous apparatus, by which it communicates with the alimentary cavity; *d*, commencement of the œsophagus and stomach; *m*, blood corpuscles; *hp*, papillæ by which the larva attaches itself.
VI. The body and the commencement of the caudal appendage of a free larva two days old. *en*, endostyle; *ks*, branchial sac; 1*ks*, 2*ks*, branchial stigmata; *bb*, entrance into the blood sinus between them; *d*, intestine; *b*, blood corpuscles; *klm*, atrial aperture.

reproductive organs are lodged in the lateral walls of the atrial cavity, and their ducts are distant from the anus; and, sometimes, there are many distinct genital glands.

In some genera, *e.g.* *Phallusia*, each egg is surrounded by an ovicapsule formed by the coalescence of cells of the epithelial lining of the ovary, and these cells may grow out into processes which give the fully formed egg a stellate appearance.

Complete yelk-division takes place, and the morula undergoes invagination (Fig. 149, I. II.). A longitudinal depression of the epiblast, extending forwards from the margins of the aperture of invagination, next makes its appearance; and, deepening, gives rise to an involution, the edges of which unite and thus shut off a tubular portion of the epiblast. This is the rudiment of the nervous ganglion (Fig. 149, III.). The aperture of invagination closes, and an outgrowth of the body gives rise to the caudal appendage, into which the urochord, formed by the coalescence of certain cells of the hypoblast, extends (Fig. 149, IV.). The sac of the hypoblast becomes divided into its branchial, œsophageal, gastric, and intestinal, portions, and the mouth

is formed by the perforation of a spot in which the hypoblast and the epiblast cohere (Fig. 149, VI.). The atrial cavity is formed by two involutions of the ectoderm, which extend inwards and apply themselves to the lateral and neural walls of the branchial sac (Fig. 149, VI.). Their originally separate apertures eventually coalesce into one.* The atrial tunic thus formed, and the walls of the branchial sac, coalesce and become perforated, in order to give rise to the stigmata.

The test appears, at first, to be a cuticular secretion of the epiblast, and to derive its cellular elements from the wandering into its substance of cells derived from the epiblast.

In *Molgula tubulosa*, Kupfer and Lacaze-Duthiers have observed that the fecundated eggs are expelled from the atrial cavity and almost immediately become fixed to the surface on which they fall. Yelk-division takes place, and after four nearly equal blastomeres are formed, much smaller ones are developed from one face of these, and increase until they constitute a blastodermic layer around

* In 1852 Krohn discovered the fact that the larva of *Phallusia* is provided with two distinct symmetrically disposed openings, by which the originally separate atria open outwards; and that the two eventually coalesce into the single atrium of the adult. Kowalewsky, Fol, and later observers, agree that these openings and the atrial sacs, are formed by two involutions of the ectoderm, which apply themselves to the sides of the pharynx, and coalesce with it at the points which become perforated by the stigmata; of which, in *Phallusia*, there are at first but two on each side. If this is a true account of the origin of the atrium, the atrial membrane is obviously part of the ectoderm, and its cavity is analogous to the pallial cavity of a mollusk.

On the other hand, Metschnikoff and Kowalewsky agree that in the buds of *Botryllus*, and other ascidians which multiply by gemmation, the two primitively distinct atrial cavities are portions of the alimentary sac, which become shut off from it, and subsequently open outwards.

Metschnikoff ("Entwickelungsgeschichtliche Beiträge," 'Bulletin de l'Acad. St. Pétersbourg,' xiii.) therefore compares the atrium to the enterocœle of Echinoderms. Renewed observations specially directed to this point, which is of great morphological importance, are much needed. If the atrial cavity is really an enterocœle, it will answer to the perivisceral cavity of the *Brachiopoda*, the pseudo-hearts of which will correspond with the primitive atrial aperture.

the larger blastomeres, which undergo a slower division. The alimentary cavity is formed by invagination. The embryos leave the egg as oval bodies, capable of undergoing considerable but slow changes of form, and devoid of any caudal appendage. Each embryo rapidly invests itself with a transparent test, throws out several tubular prolongations of the ectoderm, and finally passes into the adult condition. Although no tail is developed, a cellular mass is to be seen in the same position as that occupied by the remains of this appendage, when it has undergone its retrogressive metamorphosis, in the Ascidians with caudate larvæ. The atrial aperture is single at its first appearance, and no larval sensory organs are developed.

See page 611.

Fig. 150.—*Pyrosoma giganteum.*—I. A vertical section of the wall of the Ascidiarium near the cloacal aperture and including its lip. II. The youngest condition of a bud before the ectoderm is elevated. III. IV. V., further stages of the development of a bud. VI., a fully formed bud with a second ascidiozooid in course of development from its peduncle.

VII. A fœtus with the blastoderm divided into five segments, of which the cyathozooid (I) is the largest. VIII. A fœtus, the ascidiozooids of which half encircle the base of the cyathozooid. IX., fœtus, the most advanced stage observed. The remains of the conjoined cyathozooid and ovisac are hidden by the circle of ascidiozooids.

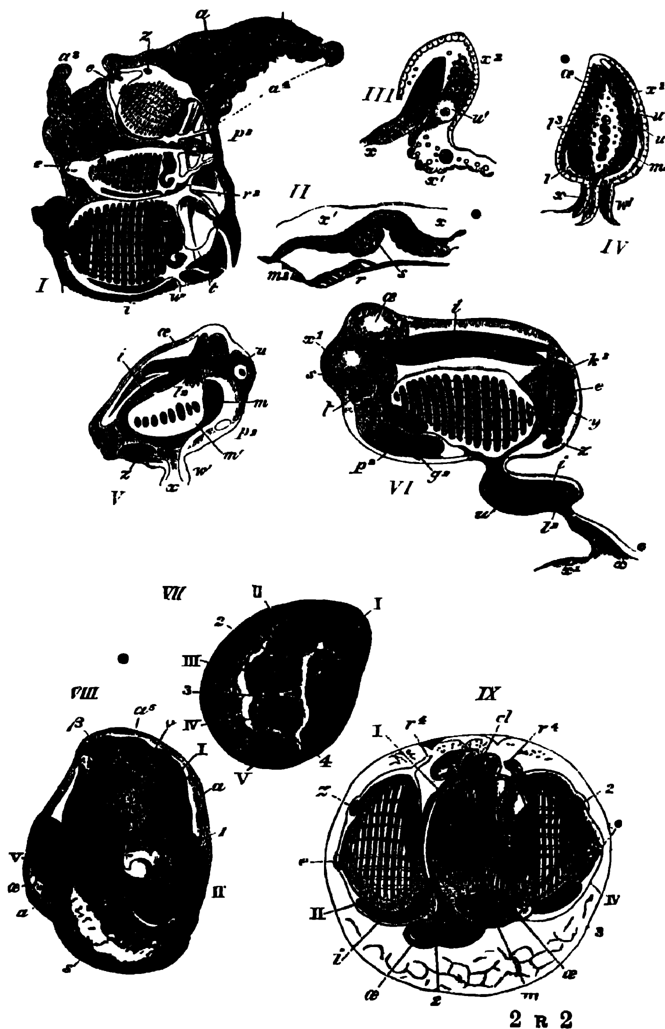
The letters have the same signification in all the figures. a, test; a^3, labial process; a^4, lip of the cloacal aperture; a^5, cells of the embryonic test; e, oral aperture; p^2, atrial aperture; i, endostyle; l^2, l^3, branchial sac and stigmata; r, heart; r^2, stolons of the adult ascidiarium; r^4, stolons of the embryonic ascidiarium; s, ovisac; t, testis; u, u', ovum; w', peduncle of a bud; x, the alimentary portion of the endoderm entering into a bud; x^1, its generative portion; x^2, the ectoderm entering into a bud; α, the œleoblast; z, ganglion.

I. II. III. IV. V. segments of the blastoderm; I, cyathozooid, IV.–V. ascidiozooids; B, mouth of the cyathozooid.

In the compound or social *Tunicata*, many ascidiozooids, which are united by a common test into an *ascidiarium*, are produced by gemmation from a solitary metamorphosed larva.

Sometimes, as in *Clavelina* and *Perophora*, the parent ascidiozooids give rise to creeping stolons, from which

Fig. 150.



branches, which develope new ascidiozooids, are given off at intervals; but, more commonly, the ascidiarium is massive, and the ascidiozooids retain no permanent connexion with one another. In the *Botryllidæ*, the zooids are arranged in whorls around a common central cavity, or *cloaca*, into which the atria of all the members of the whorl open. In *Pyrosoma*, which is a sort of floating *Botryllus*, the process of budding is highly instructive, as it exemplifies the manner in which gemmation occurs in the *Tunicata* in general.*

The *ascidiarium* of *Pyrosoma* (Fig. 150, I.) has the form of a hollow cylinder, rounded and closed at one end, truncated and open at the other, formed of a firm transparent test, in which the zooids are arranged in whorls. Their oral apertures open on the exterior surface, and their atrial apertures into the interior of the cylinder. The hæmal aspect of each zooid is turned towards the closed end of the cylinder. The branchial sac has the ordinary structure, and each zooid is provided with a testis and with an ovisac, containing a single ovum.

Every zooid multiplies by gemmation from a region of the body which lies immediately behind the extremity of the endostyle. Close to the heart, attached to a short cæcal process of the endoderm which constitutes the extremity of the endostyle, and which I have termed the *endostylic cone*, is a cellular mass—the remains of that mass of indifferent tissue which I have called the *generative blastema*, and from which the generative organs of the gemmiparous zooid have been developed (Fig. 150, II.). The endostylic cone elongates, and curving towards the hæmal side of the body, applies itself closely to the ectoderm (Fig. 150, III.). The latter grows out into a conical elevation, which projects into the surrounding substance of the test, and contains a mass of mesoblastic cells, one of which (*u'*) has already taken on the character of an ovum, and is surrounded by a rudimental ovisac. The conical bud elongates and dilates at its extremity, and the dilatation gradually takes on the form of

* Huxley, "Anatomy and Development of *Pyrosoma*." ('Trans. Linnean Society,' 1860.) Kowalewsky (*l.c.* infra, p. 616).

a new zooid united by a narrow neck, or peduncle, with the parent (Fig. 150, IV.). The endostylic cone gives rise to the whole alimentary canal of the bud, while the ectoderm of the latter proceeds from the ectoderm, and its ovisac and testis from the mesoblastic cells, of the parent. Thus the organs of the bud are all the direct product of the corresponding parts, or of the primitive layers of the germ from which they are derived, in the parent.*

After the terminal bud is formed, a second is usually developed immediately below it (Fig. 150, VI.) by the growth of the ectoderm, endodermal axis, and mesoblastic cells of the peduncle; and it would appear that this process is frequently repeated. The fully formed bud becomes detached, and takes its place among the other zooids in the test, there to repeat the process of gemmation.

The observations of Krohn, Metschnikoff, and Kowalewsky, have shown that two components enter into the buds of ascidians in general; first, an outer layer consisting of the ectoderm of the region in which the budding takes place, and secondly, an inner layer derived from the endo-

* In my second memoir on *Pyrosoma* (Trans. Linn. Society, xxiii. p. 211) I have said:—

"Gemmation does not take place in *Pyrosoma* as in so many of the lower animals (*e.g.* the *Hydrozoa* and *Polyzoa*, or *Salpa* and *Clavelina*, among the ascidians), by the outgrowth of a process of the body-wall whose primarily wholly indifferent parietes become differentiated into the organs of the bud; but, from the first, several components, derived from as many distinct parts of the parental organism, are distinguishable in it, and each component is the source of certain parts of the new being, and of them only. Thus the body-wall or external tunic of the parent gives rise to the external tunic of the bud: while a process of the endostylic cone of the parent is converted into the alimentary tract of the bud, and the reproductive organs of the latter are furnished by a part of that tissue whence the reproductive organs of the parent took their origin."

As will appear further on, however, recent investigations show that the whole process of budding in the great majority of the *Tunicata*, and at any rate the first steps of that process in *Salpa*, are essentially similar to those in *Pyrosoma*; and it remains to be seen whether there is any difference in other Ascidians. And as regards even the *Hydrozoa* the expression that the parietes of a bud are at first 'wholly indifferent' in structure is not quite accurate, inasmuch as they are composed of an ectodermal and an endodermal layer, which are continuous with those of the parent, and give rise to homologous organs.

derm of the branchial sac (*Perophora*); or, as in *Botryllus*, according to Metschnikoff, from the atrial tunic.* To these must be added a third component, derived from the indifferent tissue, out of which the reproductive organs of the parent have been developed.

In *Amouroucium proliferum*, agamic multiplication takes place when the larva has fixed itself and grown into a solitary ascidian. The long post-abdomen (as the prolongation of the abdomen beyond the alimentary canal is termed) separates itself from the body, carrying with it the heart, and divides into a number of segments which rise to the summit of the test of the parent, range themselves around it, and become converted into independent zooids. The parent developes a new heart and post-abdomen. The process appears to be repeated in the post-abdomina of the new zooids. The post-abdomen is a process of the ectoderm, the inner cavity of which is divided by a septum into two chambers, containing many fatty cells. The septum itself incloses a cavity, and there appears to be no doubt that it is a prolongation of the pharyngeal sac. When the segments of the post-abdomen develope, the cavity of the anterior end of the septum dilates and divides, as in *Didemnum*, into three chambers, of which the median becomes the branchial sac, and the lateral the atrial chambers. The rest remains as the septum of the post-abdomen of the fœtus, and its cavity at first communicates with the branchial sac, between the endostyle and the œsophageal aperture.

Kowalewsky † has observed the formation of buds from free cellular masses in the common test of *Didemnum styliferum*; the origin of these masses is undetermined. They multiply by division, after the rudiments of the alimentary cavity and of the reproductive organs have made their appearance. The alimentary cavity gives off a process whence the œsophagus, stomach and intestine are deve-

* If, as some observations tend to show, the atrial tunic itself is a diverticulum of the primitive endoderm, this case would form no exception to the general law of budding in the *Tunicata*.

† "Ueber die Knospung der Ascidien." ('Archiv für Mikr. Anatomie,' 1874.)

loped, and then becomes divided by longitudinal partitions into three chambers, a median and two lateral. The latter give rise to the lateral chambers of the atrium, which subsequently open into one another on the neural side of the body, and finally communicate with the exterior by a median atrial opening.

Gegenbaur * has described the detachment of the ova of a species of *Didemnum* into the substance of the common test, where they are developed into caudate larvæ provided with an eye. Before the development of the larva is nearly complete, a zooid is formed from it, so that, at one time, the embryo appears to have two branchial sacs.

Metschnikoff † and Krohn ‡ have shown that the caudate larvæ of *Botryllus* are not composite, as Savigny and Sars supposed, but that the bodies imagined by these observers to be buds are simply diverticula of the ectoderm, and become converted into the vascular processes, which ramify through the common test, and commonly end in dilatations. In the adult, the buds are developed, one, or sometimes two, at a time, at the sides of the body, and consist of an outer layer, derived from the ectoderm, and an inner layer, which, according to Metschnikoff, proceeds from the atrial tunic. From the inner layer the alimentary canal of the bud proceeds, and between the inner and the outer layers the rudiments of the genitalia appear. The ovaria advance towards their development much more rapidly than the testes. The zooids thus developed, as they enlarge, rise to the surface, taking the place of those from which they proceed and which die away. The ova are impregnated from without, and undergo their development in the atrium of the parent. Subsequently the testes attain their full development; and, at the same time, the buds are formed which will give rise to a third generation, supplanting the second.

* "Ueber *Didemnum gelatinosum*." ('Archiv für Anat.,' 1862.)

† "Entwickelungsgeschichtliche Beiträge." ('Bulletin de l'Académie des Sciences de St. Pétersbourg,' xiii. 1868.)

‡ "Ueber die Fortpflanzungsverhältnisse bei den Botrylliden." ('Archiv für Naturgeschichte,' (1869.) "Ueber die früheste Bildung der Botryllensstöcke." (Ibid.)

After the larva (which may be called A) has attached itself, the first sets of zooids which are developed are sexless. The first bud arises on the right side of the body of the larva (A) in the neighbourhood of the heart; as it increases in size, the parent withers away, and the zooid (B) thus developed takes its place. Two buds, a right and a left, are developed from (B) and become zooids (C,C), B disappearing. The two zooids (C, C) are so disposed that their atrial ends, are close together, and their oral ends turned away from one another. These each develope two lateral buds, which become four zooids (D, D, D, D). The zooids C, C disappear as before, and their successors arrange themselves in a circle. Each of these developes two, or sometimes three, lateral buds; these grow into zooids, which supplant their predecessors and are themselves, in turn, supplanted.

Every new system of the later successions is, at first, devoid of a common cloaca; and the zooids which compose it may arrange themselves into one or several circles, each of which then acquires its cloaca.

It thus appears that, in *Botryllus*, the ascidiozooid which results from the metamorphosis of the caudate larva serves merely as a kind of stock, from whence the other zooids which build up the ascidiarium proceed; and this leads to the still more singular process of development in *Pyrosoma*, in which the first formed embryo attains only an imperfect development, and disappears after having given rise to four ascidiozooids.

In *Pyrosoma*, the ovisac is attached by a short oviduct to the wall of the atrium, into which it eventually opens, and thus allows of the entrance of the spermatozoa.

Of the process of yelk division I could see nothing in my specimen, which was preserved in spirit, but it has since been traced in fresh specimens by Kowalewsky,* who compares it to that which takes places in osseous fishes. The result is the formation of an elongated flattened blastoderm which occupies one pole of the egg, and is

* "Ueber die Entwickelungsgeschichte der Pyrosoma." ('Archiv für Mikr. Anatomie,' 1875.)

converted into what I termed the *cyathozooid*, which is shown by Kowalewsky to be a sort of rudimentary ascidian (Fig. 150, VIII.). From this, a prolongation or stolon is given off, which becomes divided by lateral constrictions into four portions, each of which gives rise to a complete ascidiozooid. As these increase in size, they coil themselves round the cyathozooid, with their oral openings outwards and their cloacal openings inwards, and thus lay the foundation of a new *ascidiarium* (Fig. 150, VIII.). The cyathozooid eventually disappears, and its place is occupied by the central cloacal cavity (Fig. 150, IX.). Thus, in *Pyrosoma*, the usual first stage of an Ascidian—the caudate larva—is abortive and serves only to found the colony by the buds which are developed from it.

In the pelagic genus *Doliolum* * the cycle of life of the species is represented by distinct sexual and sexless forms. The egg produced by the sexual form (A) † gives rise to a caudate larva which passes into the first sexless form (B); this gives off from the neural side of the body an outgrowth or stolon, from which buds are developed. These buds are arranged in three rows, two lateral and one median, and grow into zooids of two different forms, of which the median may be indicated by C *m*, the lateral by C *l*. All these zooids are detached, and swim about as independent organisms. What becomes of the lateral zooids (C *l*) is unknown. But the median zooids give off a stolon from the hæmal side of the body on which buds are developed, which pass into the sexual form (A).

The sexual zooid (A) (Fig. 151) is shaped like a cask with an opening at each end; these are the oral and cloacal apertures. According to Keferstein and Ehlers there is no test, the outer wall of the body being formed, as in most *Appendiculariæ*, by the ectoderm. Eight muscular bands

* Huxley, "Remarks upon *Appendicularia* and *Doliolum*." ('Phil. Trans.,' 1851.) Krohn, "Ueber die Gattung *Doliolum*." ('Archiv für Naturgeschichte,' 1852.) Gegenbaur, "Ueber die Entwickelung von *Doliolum*." ('Zeitsch. für Wiss. Zoologie,' 1853.)

† Keferstein und Ehlers, 'Zoologische Beiträge,' 1861.

encircle the body, and by their contractions expel the water from either the oral or the cloacal ends. The body is thus propelled either backwards or forwards. The branchial sac is much simplified. In *Doliolum Mülleri*, the atrial cavity does not extend further forwards than the hinder end of the wide pharynx, and this is perforated only by two rows of stigmata, four or five in each. In *Doliolum denticulatum* (Fig. 151), on the other hand, the atrial cavity extends forwards at the sides of the pharynx, both on the hæmal and the neural side, and the stigmata are numerous and vertically elongated.

An opening in the middle line of the hæmal face of the

Fig. 151.

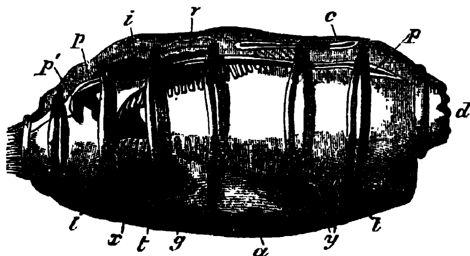


Fig. 151.—*Doliolum denticulatum.*—*a*, ganglion; *c*, endostyle; *d*, oral opening; *g*, œsophagus; *i*, stomach; *l*, intestine; *p*, *p'*, testis; *r*, heart; *t*, *t*, muscles.

pharynx leads, by a short gullet, into a dilated stomach, whence the slender intestine proceeds to terminate in the atrial cavity. The nervous ganglion is situated in the third intermuscular space in *D. denticulatum*. There is a ciliated sac, but no auditory organ, in the sexual form. The testis is a long tube (Fig. 151, *p*, *p*), which lies on one side of the hæmal face of the body and opens on a papilla in the atrium. The ovary, small, rounded, and situated close to the hinder end of the testis, contains many ova. According to Keferstein and Ehlers, the ova and spermatozoa appear often to become ripe at the same time.

The first sexless zooid (B) resembles A in general form, but has nine muscle-rings. The long stolon, which trails in the water, is attached in the seventh intermuscular space to the middle of the neural face of the body. The stigmata are arranged as in the form A, of *Doliolum Mülleri*, and one of the antero-lateral nerves terminates in an otolithic sac. It is spherical and contains a single otolith.

The zooids produced by the lateral buds of the stolon (C *l*) have wide oral apertures, and the body is shaped somewhat like the bowl of a spoon. They possess neither auditory organs nor genital organs, nor have they been observed to develope buds. The median zooids (C *m*) closely resemble the sexual zooids. The stalk by which each is attached, and the insertion of which is in the middle line of the hæmal face in the sixth intermuscular space, remains as a prominence after the animal is set free; and, from the base of this prominence, buds are developed, which take on the sexual form (A).

In the *Salpæ*, the divergence from the ordinary *Tunicata* reaches its maximum. The oral and atrial openings are situated at opposite extremities of the body, as in *Pyrosoma* and *Doliolum*; and the branchial stigmata are represented by wide vacuities at the sides of the branchial sac, the walls of which are thus represented only by the epipharyngeal folds on the one side, and a narrow trabecula, which occupies the region of the hypopharyngeal band, on the other side. The relatively small alimentary and reproductive viscera are sometimes aggregated into a mass, the so-called *nucleus*, at the posterior end of the hæmal side of the body. The chief muscular bands, by the contraction of which the water is driven out of the branchial and atrial apertures, and the propulsion of the animal is effected, are transverse, but do not form complete hoops, as in *Doliolum*.

In all the *Salpæ*, each species is represented by two sets of zooids, the one sexual and the other sexless. The sexual zooids are produced by budding from a stolon, which is given off from the body of the sexless form in the immediate neighbourhood of the heart. When the sexual zooids thus

formed are detached, they are at first connected into chains of various forms, but these eventually break up and the constituent zooids are set free. Fig. 152 shows the two zooids of the species *Salpa democratica-mucronata*, viz. the sexless zooid, *Salpa democratica* (Fig. 152, I.) and the free sexual zooid, *Salpa mucronata* (Fig. 152, II.).

The recent investigations of Dr. Todaro,* in accordance with those of Kowalewsky, show that the stolon is formed, as in *Pyrosoma*, by the conjunction of a process of the endoderm which forms the extremity of the endostyle, with an outgrowth of the ectoderm, and with certain cells of the mesoblast. But, according to Todaro, there is this essential difference: the young *Salpæ*, which make their appearance in double series along the stolon, are developed altogether from the mesoblastic cells. These cells, in fact, become aggregated into masses, of which four are arranged in the circumference of each segment into which the stolon is divided; and two of these masses, one on each side of each segment, are converted into young *Salpæ*, by a process analogous to that by which a morula becomes an embryo. If this account of the matter be correct, the agamic development of the *Salpæ* would rather resemble that of the germ masses of the sporocysts of *Trematoda*, or the pseudova of insects, than ordinary budding.

Each sexual zooid possesses a testis and a single ovum. The latter is contained in an ovarian follicle, the slender duct of which is attached to the wall of the atrium and opens into the atrial cavity. The testis attains its full growth and functional perfection only after the ovum has undergone development. It follows, therefore, that impregnation must be effected by the spermatozoa of some other zooid. The sexless form which is developed from the egg, goes through the early stages of its development in the atrial cavity of the parent, to the walls of which it is attached by a peduncle (Fig. 152, III.), the centre of which is occupied by a diverticulum of the vascular canals of the parent, enclosed within a cup-shaped cavity in free communication with the blood

* 'Sopra lo Sviluppo e l'Anatomia delle Salpe,' 1875.

Fig. 152.

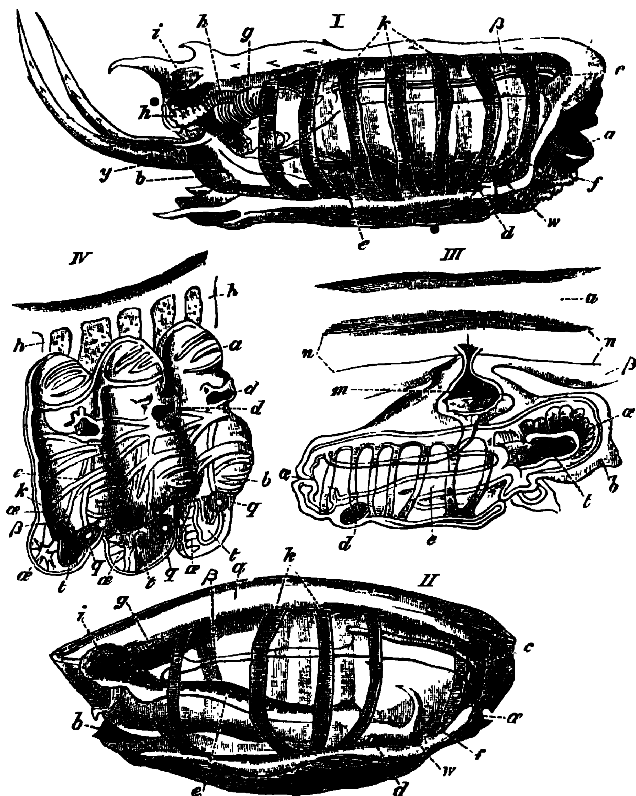


Fig. 152.—*Salpa democratica-mucronata.*—I. *Salpa democratica.* II. *Salpa mucronata.* III. A fœtal *Salpa democratica* attached by its placenta to the wall of the atrial cavity of a *Salpa mucronata.* IV. Part of the stolon of *Salpa democratica* with attached *Salpa mucronata* buds.

The letters have the same signification throughout. *a*, oral; *b*, atrial orifices; *c*, endostyle; *d*, ganglion; *e*, hypopharyngeal band in a so-called 'branchia;' *f*, languet; *g*, heart; *h*, gemmiparous stolon; *i*, visceral mass or nucleus; *k*, muscular bands; *m*, placenta; *n*, blood sinus; *q*, ovisac and ovum; *t*, stomach; *w*, ciliated sac; *œ*, œleoblast; *α*, ectoderm and test; *β*, endoderm.

sinuses of the fœtus. It is, in fact, a true *placenta;* and, during life, the independence of the fœtal and maternal circulations is readily observed, as the blood corpuscles of the two organisms course through their respective channels.

The early stages of the development of the embryo *Salpa* have been investigated by numerous observers, most recently by Kowalewsky,* Todaro, Brooks † and Salensky.‡ The observations of the last-named author relate chiefly to *Salpa democratica-mucronata*, and his account of the process appears to me to be the most satisfactory.

The egg is impregnated in the ovarian follicle, as in *Pyrosoma;* and the oviduct, shortening, gradually draws the ovarian follicle, with its contents, into a sort of incubatory pouch, which is a diverticulum of the wall of the atrium, and projects into the atrial cavity.

For distinction's sake the incubatory pouch may be termed the *ovicyst*. As the oviduct shortens, it widens and constitutes, together with the ovarian follicle, a single *uterine sac*, the outer or oviducal half of which applies itself to the wall of the ovicyst, while the inner half contains the ovum. The vitellus undergoes complete division, and the superficial layer of blastomeres constitutes itself into an epiblast, investing the solid mass formed by the other blastomeres, which represent the hypoblast. A mesoblastic layer subsequently appears between the two. The nervous ganglion results from an involution of the epiblast, while the branchial sac, the alimentary canal and the atrium are the product of the subdivision of a cavity which appears in the midst of the hypoblast. The maternal and the fœtal parts of the placenta arise, respectively, from the wall of the ovarian sac and from certain large blastomeres on the adjacent hæmal face of the embryo.

Todaro agrees with other observers in stating that the vitellus undergoes division, and that a small celled blasto-

* 'Nachrichten der Königlichen Gesellschaft zu Göttingen,' 1868.

† 'Bulletin of the Museum of Comparative Zoology,' No. 14.

‡ 'Zeitschrift für Wiss. Zoologie,' 1876.

derm invests the large remaining cells which he terms the *germinal mass*. But his account of the further stages of development is very different. A circular thickening of the blastoderm separates the hemisphere which is directed outwards from that which is turned inwards, and gives rise to a lamellar outgrowth. It is, at first, directed towards the inner end of the ovisac, having reached the bottom of which, it becomes reflected; and the reflected portions lining the inner wall of the ovisac, and meeting over the outer hemisphere, form a sort of amniotic investment of the embryo. It is the cavity left between this 'amnion' and the inner hemisphere of the blastoderm which becomes the parental blood sinus. An involution of the outer hemisphere of the blastoderm gives rise to the alimentary canal, which becomes shut off, as the endoderm, from the remaining blastoderm, which constitutes the ectoderm. A mass of cells which appears in the middle of the outer half of the embryo, between the alimentary sac and the ectoderm, and which has only a transitory existence, is regarded by Todaro as the representative of the urochord.

CHAPTER XI.

THE PERIPATIDEA, THE MYZOSTOMATA, THE ENTEROPNEUSTA, THE CHÆTOGNATHA, THE NEMATOIDEA, THE PHYSEMARIA, THE ACANTHOCEPHALA AND THE DICYEMIDA.

I HAVE reserved for discussion in this Chapter the *Peripatidea,* which have heretofore been referred by most authors to the *Annelida;* and certain groups of the lower *Metazoa,* the precise morphological relations of which are as yet uncertain, although it is pretty clear that several of them are allied with the lower *Annelida,* the *Rotifera,* and the *Turbellaria.* They are, for the most part, totally devoid of segmentation; while the *Chætognatha* and the *Myzostomata* alone present any structures resembling limbs, though the nature of these is doubtful. So far as the nervous system is clearly made out, it exhibits no such chain of post-oral ganglia as characterises the higher worms.

The PERIPATIDEA.—At p. 257, I have referred this group to the *Arthropoda,* Mr. Moseley's memoir on *Peripatus** having left no doubt upon my mind, that he had satisfactorily proved the justice of the surmise respecting its affinities originally made by Gervais. It is only recently, however, that I have been able, thanks to Mr. Moseley, to examine one or two specimens of *Peripatus Novæ Zelaniæ,* and to satisfy myself of the main point, namely the existence of the tracheal system which he has described.

Of the genus *Peripatus* several species are now known,

* 'Philosophical Transactions,' 1874. See also the valuable memoir of Grube, "Ueber den Bau von *Peripatus Edwardsii.*" ('Archiv für Anatomie,' 1853.)

from the West Indies, South America, the Cape of Good Hope and New Zealand, where they are found among the decaying wood of damp and warm localities. They have the curious habit of throwing out a web of viscid filaments when handled or otherwise irritated.

The head is distinct, and is provided with a pair of many-jointed antenna-like tentacula and two simple eyes. The mouth, situated upon the under surface of the head, is surrounded by a prominent lip, which encloses a pair of jaws, each of which is terminated by two curved chitinous claws, similar to those of the feet. On each side of the mouth, the head supports a short obscurely jointed 'oral papilla,' which is somewhat like one of the feet, but is devoid of claws and perforated at its extremity. The head is followed by an unsegmented body produced laterally into paired appendages, which vary in number from fourteen to more than thirty, according to the species; and each of these appendages is indistinctly articulated, the terminal joint being provided with two small curved claws.

The anus is terminal and the genital aperture is situated on a papilla, a little distance in front of the anus, on the neural or ventral face of the body.

The alimentary canal commences by an ovoid muscular pharynx. The œsophagus, continued from this, gradually dilates into a wide and long stomach, from which a very short intestine is continued to the anus, situated at the posterior end of the body. There are no Malpighian cæca. Two very large ramified tubular glands, which secrete the viscid matter of which the web is composed, lie at the sides of the alimentary canal, and open outwards by the perforations of the oral papillæ. A vessel occupies the middle line of the dorsal body-wall, and is probably a heart.

The respiratory organs are the tracheæ discovered by Mr. Moseley. The numerous pores, or *stigmata*, from which the tracheæ take their origin, are scattered all over the surface of the body, one row being median and ventral. Each stigma is the outward termination of a short wide tube, which, at its opposite end, branches out into a pencil

of fine tracheæ, which rarely divide, and are distributed in great abundance to the viscera. They are very delicate tubes, which often take an undulating course, and are rarely more than $\frac{1}{7000}$th of an inch in diameter. In optical section, their walls have a finely beaded appearance, as if from the presence of transverse thickenings, though distinct transverse markings are rarely to be seen.

The nervous system, as Milne-Edwards discovered, consists of two ganglia in the head, closely united above the œsophagus. From each of these a relatively stout longitudinal cord proceeds, overlying the bases of the feet (and hence widely separated from its fellow) to the posterior extremity of the body. As Grube has stated, there are no distinct ganglia on this cord. On the contrary, ganglionic cells appear to be pretty evenly distributed along its ventral face, throughout its length; and nerves, which pass transversely outwards and inwards, are given off from opposite sides of it at short intervals. Grube has shown that many of the branches that take the latter direction are commissures between the two cords.

The muscles of *Peripatus* are not striated, which is a curious exception to its generally well-marked arthropod characteristics.

Mr. Moseley has proved that the sexes are distinct. The ovary is small, divided by a median septum into two lobes, and lies beneath the alimentary canal. The oviduct, at first single, divides into two branches, which are long, and, posteriorly, present uterine dilatations. They then unite, and terminate by a short vagina on the ventral aspect of the rectum. The testes are ovate bodies, each with a cæcal appendage. The long and coiled vasa deferentia unite into a common duct, which opens in the same position as in the female. The ova are developed within the uterine dilatations of the oviducts.*

* One of the specimens which I examined was a pregnant female, but the viscera were glued together, apparently by the action of the spirit in which it had been preserved, in such a manner, that little could be made of their structure or of that of the embryos.

Mr. Moseley has made out the chief points in the developmental history of *Peripatus*.

In an early condition, the embryo is very like that of a Scorpion, but is folded upon itself, so that the ventral aspects of the anterior and posterior halves of the body are turned towards one another. As in the Scorpion, there is a pair of large procephalic lobes, succeeded by a series of segments, from the sides of which, processes—the rudiments of the limbs—bud out. The procephalic lobes give rise to a kind of hood, the lateral angles of which extend over the bases of the first pair of limbs, and join with those of the second pair, which are the oral papillæ of the adult. The first pair of limbs thus become enclosed within the hood (the margins of which form the suctorial lip of the adult), and developing two chitinous claws upon their extremities, like those of the other limbs, they are converted into the jaws of the adult animal. It is remarkable that the antennæ are developed from the anterior part of the procephalic lobes; while the cheliceræ of the Scorpion appear at the posterior margin of these lobes, in a position corresponding with that of the first pair of limbs, or jaws, of *Peripatus*.

It is obvious that whether we consider the appendages, the respiratory and reproductive systems, or the development of the embryo, *Peripatus* is a true Arthropod, apparently nearly allied to the suctorial *Myriapoda*.

The MYZOSTOMATA.—The genus *Myzostomum** comprehends certain small animals, the largest species not exceeding $\frac{1}{5}$th of an inch in length, which are parasitic upon the Feather-stars. The body has the form of a flattened oval disk, the surface of which is ciliated, while its margins may be produced into as many as twenty short filamentous processes or cirri. Within the margin of the ventral face are eight suckers, four on each side, and, internal to these again, are ten short conical 'feet,' five on each side; each of these lodges two strong setæ, which can

* See Lovén, 'Archiv für Naturgeschichte,' 1842.

be protracted and retracted in the same way as those of Annelids. Just within the middle of the anterior margin lies a rounded aperture, through which a muscular proboscis, the free end of which is beset with papillæ, can be protruded. A straight alimentary canal runs through the body, and terminates in a sort of cloaca, which opens in the middle line on the posterior margin. From each side of the alimentary canal long ramified cæca are given off.

No vessels or organs of circulation have been discovered. All that is known of the nervous system is an elongated ganglionic mass, from which branches are given off on each side, situated in the middle line of the ventral face of the body.

The sexes are combined in the same individual. The acini of the generative glands are scattered through the body. Those of the testes pour their contents into ducts, which unite together and open by a separate vas deferens on each side of the body, about the middle of its ventral face. The two oviducts convey the ova to the cloacal chamber.

The development of *Myzostomum* has been worked out by Semper and by Metschnikoff.* The vitellus undergoes complete division, and the embryo leaves the egg as an oval morula, covered with vibratile cilia. In the next stage observed, the embryo is cylindroidal, and is provided with a mouth at one end and an anus at the other. The commencement of the straight and simple alimentary canal has the form of a muscular bulb or proboscis. There are two pairs of rudimentary appendages, each containing two setæ. The number of the setigerous appendages increases up to five pairs, and the intestine begins to show indications of diverticula; but, in the latest stage observed, the cirri had not made their appearance, and the body was still comparatively narrow.

Metschnikoff regards *Myzostomum* as a parasitic form of a polychætous Annelid; and there is much to be said in favour of this suggestion; though, in some respects, it rather approaches the *Hirudinea*.

* Semper, "Zur Anat. und Entwickelungsgeschichte der Gattung Myzostomum." ('Zeitschrift für Wiss. Zoologie,' 1875.) "Zur Entwickelungsgeschichte von Myzostomum" (*Ibid.* 1866).

The presence of cilia on the surface of the body and of protractile setæ in the parapodia excludes *Myzostomum* from the *Arthropoda;* while Metschnikoff has justly compared its larval state with that of *Syllis.* Sufficient doubt, however, still adheres to the determination of the true place of *Myzostomum,* to lead me to discuss it apart from the Annelids.

The ENTEROPNEUSTA.—The very singular animal *Balanoglossus,* which is the only known example of this group, is an elongated, apodal, soft-bodied worm, with the mouth at one end of the body and the anus at the other (Fig. 153, III.) The mouth is surrounded by a sort of collar or prominent lip, within the margin of which springs a long proboscidiform median appendage, which is hollow within and has a terminal pore. On the same side as that from which the proboscis springs, the anterior region of the body presents an elongated, somewhat flattened area, bounded by raised longitudinal folds. On each side of this area is a longitudinal series of apertures—the *branchial apertures.* The latter communicate with saccular dilatations of the anterior part of the alimentary canal, and these *branchial sacs* are supported by a peculiar skeleton.

No nervous system, nor any organs of sense have yet been certainly made out.

According to Kowalewsky,* who was the first to elucidate the true nature of *Balanoglossus,* the vascular system consists of a dorsal and a ventral vessel. At the posterior end of the branchial region, the former divides into a superior and an inferior dorsal, and two lateral, trunks. The superior trunk passes forwards; and, at the anterior end of the body, divides into two descending branches, which unite with the ventral trunk. The inferior dorsal trunk supplies the branchiæ, of which the lateral trunks are the efferent vessels.

For the pharyngeal branchiæ of *Balanoglossus,* the only

* 'Anatomie des Balanogossus.' ('Mém. de l'Acad. Imp. de St. Pétersbourg,' 1866.)

parallels to be found are among the *Tunicata* and the *Vertebrata.* On the other hand, the larval form of this anomalous creature is generally Annelidan or Turbellarian, with very close and special resemblances to the Echinopædia of some *Echinodermata.*

The young of *Balanoglossus* was first observed by Müller, who called it *Tornaria*, and regarded it (as did all succeeding observers, until its true nature was discovered) as an Echinoderm-larva, on account of its extraordinary resemblance to the larvæ of some Star-fishes (Fig. 153, I.).

It is an elongated ovoid body, provided with three bands

Fig. 153.

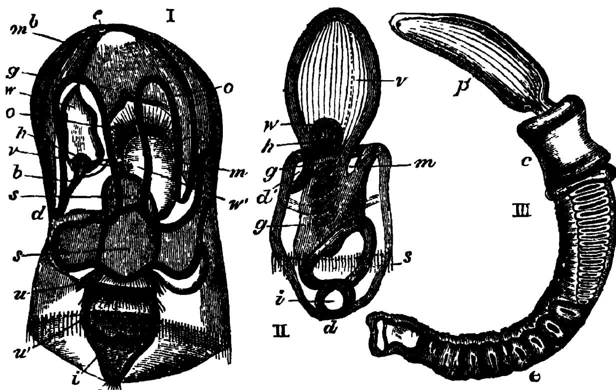


Fig. 153.—*Balanoglossus.* (After A. Agassiz.)
I. The *Tornaria* larva, side view (about $\frac{1}{12}$ of an inch long). *a*, anus; *b*, vessels leading to the dorsal pore (*d*) from *w*, the sac of the water-vascular system; *w'*, prolongation of the sac; *h*, heart; *i*, intestine; *s*, stomach; *o*, œsophagus; *m*, mouth; *u*, *u'*, lobes of the alimentary canal; *mb*, muscular band running from the eyespeck (*e*) to the water-vascular sac.
II. A young *Balanoglossus*—letters as before except *g*, the first formed branchial stigmata.
III. A more advanced *Balanoglossus*; *e*, the collar; *p*, the proboscis.

of cilia, one of which is præ-oral, while the other two are post-oral. Of the latter, one, at the posterior end, is circular, while the other is inclined obliquely to the axis of the body, so that anteriorly and superiorly it reaches the anterior

extremity, while posteriorly it occupies nearly the middle of the body. On the ventral face, a deep groove separates it from the præ-oral ciliated band, and in this groove the mouth is situated. The margins of the præ-oral and post-oral ciliated bands are deeply sinuated, and they come into contact in the median dorsal line. A wide gullet leads from the mouth, and opens into the gastro-intestinal portion of the alimentary canal, which passes backwards in the middle line, to terminate in the anus, at the hinder end of the body. About the middle of the dorsal face of the body there is a circular pore (Fig. 153, I *d*), whence a canal leads to a rounded sac, which lies on the junction between the gullet and the stomach. The sac gives off two lateral short diverticula, which embrace the œsophagus. A delicate band, apparently of a muscular nature, connects the summit of the water-sac with that part of the dorsal aspect of the body at which the præ-oral and post-oral ciliated bands unite. Here two eye-spots are developed. A constriction separates a rounded gastric, from a tubular intestinal, division of the alimentary canal. Diverticula of the gastro-intestinal part of the alimentary canal give rise to two pairs of discoidal bodies, from which, apparently, the mesoblast and the perivisceral cavity of the *Balanoglossus* are developed.

From the sides of the œsophagus, a series of diverticula are given off, which unite with the ectoderm, open externally, and become the gill-pouches. When only two of these branchial apertures are formed, they are said by Metschnikoff to have a striking resemblance to those of *Appendicularia.* A pulsating vesicle—the so-called "heart,"—makes its appearance close to the water-sac. The anterior end of the body, in front of the mouth, now elongates, and is converted into the proboscis; while the post-oral region loses its ciliated bands, and lengthening, becomes the long body of the adult worm.* (Fig. 153, II. III.)

* See Agassiz, "The History of *Balanoglossus* and *Tornaria,*" ('Memoirs of the American Academy of Arts and Sciences,' 1873); and Metschnikoff, "Untersuchungen über die Metamorphose einiger Seethiere." ('Zeitschrift für Wissenschaftliche Zoologie,' xx. 1870.)

The CHÆTOGNATHA.—The genus *Sagitta*,* which is the only member of this group, comprises several species of small animals which are found swimming at the surface of the ocean in all parts of the world. Although the whole structure and course of development of *Sagitta* are now very well known, its true affinities are not definitively settled. Anatomically, it approaches the Nematoid worms and the oligochætous Annelids in some respects; but its development presents peculiarities which are as yet unknown among these animals, while they occur among the *Brachiopoda* and the *Echinodermata*.

The body of *Sagitta* (Fig. 154) rarely more than an inch long, is elongated, subcylindrical and unsegmented; it is enlarged at one end into a rounded head, while at the other it tapers to a point. There are no parapodial appendages, but the chitinous cuticle is produced into a finely striated lateral fin, on each side of the body and tail, and into delicate setæ. On each side of the head there are a number of strong, curved, claw-like chitinous processes, which can be laterally divaricated and approximated, and serve as jaws. Between them is the mouth; and, at the sides of the mouth, are four sets of short but strong spines. The mouth leads into a simple and straight intestine, which opens by an anus situated on the ventral face of the body, where the tapering caudal region commences. A dorsal and a ventral mesenteric band connect the intestine with the wall of the body, and divide the perivisceral cavity into two chambers. Beneath the ectoderm lies a layer of longitudinal, striated, muscular fibres. The nervous system consists of a large oval ganglion, which lies in the middle of the ventral wall of the body, and sends off anteriorly two commissural cords, which unite with a supra-œsophageal ganglion. Among other branches, this gives off two to the dorsal side of the head; these dilate at their extremities into spheroidal ganglia on which the eyes rest. The ovaries are elongated tubular organs, which lie one on each side of the intestine,

* See Busk, 'Quarterly Journal of Microscopical Science,' 1856. Leuckart and Pagenstecher, 'Archiv für Anatomie,' 1858.

attached to the parietes of the body. Their ciliated ducts open close to the vent and are provided with dilatations

Fig. 154.

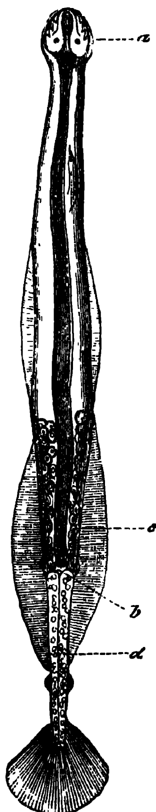


Fig. 154.—*Sagitta bipunctata.*—*a*, the head with its eyes and appendages; *b*, the anus; *c*, the ovary; *d*, the testicular chambers.

which serve as receptacula seminis. Behind the anus, the mesenteric laminæ unite and form a vertical partition,

which divides the cavity of the caudal part of the body into two chambers. On the lateral walls of these, cellular masses are developed, which become detached, and, floating freely in the perivisceral fluid, are developed into spermatozoa. The latter escape by spout-like lateral ducts, the dilated bases of which may be regarded as vesiculæ seminales.

Thus far, although the organisation of *Sagitta* is very peculiar, it presents analogies both with the *Nematoidea* and with the *Annelida*. But its development, as described by Kowalewsky,* is, in some respects, unlike anything at present known in either of these groups. Yelk-division takes place, as usual, and converts the egg into a vesicular morula, with a large cleavage cavity, or blastocœle. One face of the vesicle thus constituted now becomes invaginated, with the effect of gradually obliterating the blastocœle, and converting the spherical single-walled sac into a hemispherical, double-walled, cup-shaped gastrula. The cavity of the cup is the future digestive cavity; the layer of invaginated blastodermic cells which lines this cavity is the hypoblast, which will become the endoderm; and the outer layer of cells is the epiblast, and will become the ectoderm. In this condition, the embryo resembles that of the Leech in its early state. The embryo elongates, and the aperture of invagination, or blastopore, eventually ceases to be discernible. Whether it becomes the anus, or whether the anal aperture is formed anew, is not certain. The nervous ganglia result from the modification of cells of the ectoderm. The anterior end of the primitive alimentary cavity, or archenteron, is at first closed. It soon sends out an enlargement on each side, so that the archenteron is divided into a central and two lateral divisions. The central division opens externally and anteriorly by the development of the oral aperture; and, as the body elongates, it becomes the tubular intestine. The lateral diverticula at first communicate with it, but they are eventually shut off, and constitute the right and left

* 'Mémoires de l'Academie Imperiale des Sciences de St. Pétersbourg,' 1871.

perivisceral cavities, their walls becoming converted into the cellular and muscular lining of those cavities. It results, from the mode of development of the perivisceral cavity of *Sagitta*, that this cavity, like the perivisceral cavity of the Brachiopods and the "peritoneal" cavity of the Echinoderms, is an enterocœle, comparable to that of the *Hydrozoa* and *Actinozoa*; but which, instead of remaining in communication with the alimentary cavity, is shut off from it, its wall becoming the mesoderm, and its cavity the perivisceral cavity.*

Nothing of this kind is known to occur in the *Turbellaria*, *Annelida*, *Nematoidea*, or *Rotifera*; but when a perivisceral cavity exists in these animals, it appears always to result from the excavation of the, at first, solid mesoblast. The perivisceral cavity thus developed is what I have termed a *schizocœle*. But whether there is any fundamental difference between an *enterocœle* and a *schizocœle* is a matter for further inquiry. I have referred above (p. 565) to the case of an Ophiurid, in which the hollow diverticula of the archenteron, characteristic of the Echinoderms, are represented by solid outgrowths of the hypoblast. From this condition there would appear to be an easy transition to that presented by the embryos of those *Oligochæta* and *Hirudinea*, in which, though the mesoblast is a product of the hypoblast, it contains no continuation of the alimentary cavity, but eventually splits into a visceral and a parietal layer, the interval between which is the perivisceral cavity; and there is much probability in Kowalewsky's suggestion that the longitudinal bands

* Kowalewsky's account of the development of *Sagitta* has been confirmed by Bütschli [1] who has further determined the origin of the reproductive organs, which arise as outgrowths from the hypoblast; and the division of each primitive enterocœle into two sacs, one for the head, and another for the body. It appears probable that the latter becomes subdivided by a transverse partition between the ovary and testis. Bütschli suggests that the segmentation of the mesoblast, which forms the walls of the enterocœle, is a point of approximation between *Sagitta* and the Annelids.

1 "Zur Entwickelungsgeschichte der Sagitta." ('Zeitschrift für Wiss. Zoologie,' 1873.)

(*Keimstreifen*) in which the mesoblast makes its appearance, may be homologous with the diverticula of the alimentary cavity of *Sagitta*.

In this case, the schizocœle will be an advance upon the enterocœle, and the development of the perivisceral cavity in *Sagitta* may represent the primitive mode of development of all invertebrate perivisceral cavities. On the other hand, it must be remembered that between the endoderm and the ectoderm in the disk of a Medusa, or in the body of a Ctenophoran or Turbellarian, there is a gelatinous mesoderm which occupies the position of the primitive blastocœle. Now, this mesoderm may be, and probably is, a product of the endoderm; but any cavities which appear in it, such, for example, as the water-vascular canals of the *Turbellaria*, can have nothing to do with an enterocœle.

Again, in the *Tunicata*, as we have seen, the atrium is a kind of "perivisceral cavity," which is formed either by an invagination of the ectoderm, in which case it may be termed an *epicœle*; or else it is a true enterocœle. Assuming the former alternative, for the moment, to be that which ought to be adopted, what is called a "perivisceral cavity" may be one of four things:—

1. A cavity within the mesoblast, more or less representing the primitive *blastocœle*.

2. A diverticulum of the digestive cavity, which has become shut off from that cavity (*enterocœle*).

3. A solid outgrowth, representing such a diverticulum, in which the cavity appears only late (modified *enterocœle* or *schizocœle*).

4. A cavity formed by invagination of the ectoderm (*epicœle*).

And whether any given perivisceral cavity belongs to one or other of these types can only be determined by working out its development.

The NEMATOIDEA.—The "Thread-worms" have elongated rounded bodies, which usually taper towards one or both ends; they are not divided into segments, and they

are devoid of limbs, though they may occasionally be provided with setiform spines or papillæ. In *Desmoscolex*, the papillæ and setæ acquire an almost Annelidan aspect, and the annulation of the body is much more distinct than in any other Nematoid Worm.

Fig. 155.

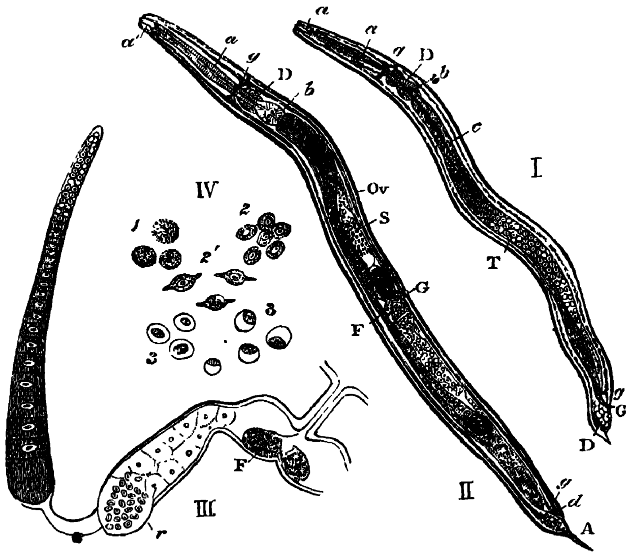


Fig. 155.—*Anguillula brevispinus* (after Claus).*
I, male; II, female; III, female genital organs; IV, seminal corpuscles in different stages of development.
a, œsophagus; *a'*, chitinised oral capsule; *c*, gastric, and *d*, rectal portion of the alimentary canal. A, anus; *gg'*, anterior and posterior thickenings with their commissures; G, sexual aperture; F, fatty-looking gland; *r*, dilatation of the uterus, serving as a receptaculum seminis. D, unicellular cutaneous glands at the anal extremity; D', glandular mass with its excretory duct above the gizzard; *ov*, ovarium; T', testis; S, seminal corpuscles.

The outermost layer of the body is a dense chitinous cuticula, usually divisible into several layers. These layers

* "Ueber einige in Humus lebende Anguillulinen." ('Zeitschrift für Wiss. Zoologie,' xii.)

may be fibrillated, the direction of the fibrillation being different in the successive layers. Cilia are found neither on the surface, nor elsewhere, at any period of life. The mouth is situated at one extremity of the body, the anus at, or near, the other end. The first portion of the alimentary canal is a thick-walled pharynx, lined by a continuation of the chitinous layer of the integument, which may be raised up into ridges or tooth-like prominences. Transverse fibres, apparently of a muscular nature, radiate from the lining of the pharynx through its thick wall, and probably serve to dilate its cavity. A straight and simple tubular alimentary canal, without any distinction into stomach and intestine, extends through the axis of the body, a narrow œsophageal portion usually connecting it with the pharynx.

The endoderm, or wall of the alimentary canal, consists of a single layer of cells, disposed in few or many longitudinal series; and lined, both internally and externally, by a cuticular layer. On each side, the intestine is fixed through its whole length to the "lateral area," to be described below. The cuticle, which lines the inner faces of the endodermal cells, and circumscribes the digestive cavity, appears, on vertical section, to be divided into rods, which are possibly merely the intervals of minute vertical pores. In some cases, muscular fibres invest the posterior portion of the intestine.

Beneath the layers of the chitinous cuticle there is a proper integument, or ectoderm, internal to which again is a single layer of longitudinally-disposed muscles, which may or may not be divided into distinct series of "muscle-cells." The space between these and the outer face of the intestine is occupied by a spongy or fibrous substance, which must probably be regarded as a kind of connective tissue. The muscles and this tissue, taken together, constitute the mesoderm.

In the typical *Nematoidea*, the muscular layer does not form a complete investment of the body, but is interrupted along four equidistant longitudinal lines. One of them is termed dorsal, the opposite ventral, and both these are very

narrow. The other two are much broader, and are termed the lateral areas. They often (Fig. 156) present two or more series of conspicuous nuclei, and each is traversed by a canal with well-defined contractile walls and clear contents. Opposite the junction of the œsophageal with the gastric portion of the alimentary canal, each of these lateral canals passes inwards and towards the mid-ventral line, and, joining with its fellow, opens by a pore on the exterior. In some cases, continuations of the lateral canals extend forwards into the head.

A ring of fibres and nerve-cells surrounds the gullet,

Fig. 156.

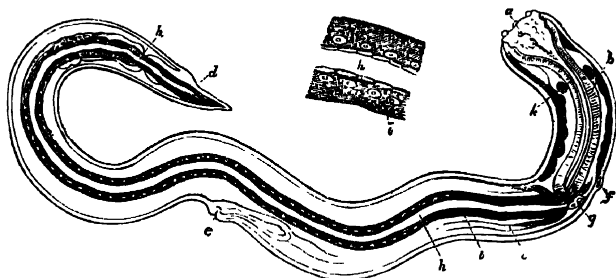


Fig. 156.—*Oxyuris.*—*a* Mouth. *b.* Pharynx. *c.* Commencement of intestine, and *d*, its termination. The intermediate portion is not figured. *e.* Genital aperture. *f.* Opening of vessels, *g.* Their receptacle. *h.* One of the vessels. *i.* Cellular matter enveloping them. A portion of one of the contractile vessels is represented more highly magnified in the upper figure.

about the level of the opening of the water-vascular system, and gives off filaments forwards to the head, and backwards to the muscles and to the lateral area; while two cords pass back, along the dorsal and ventral median lines, to the hinder end of the body. In the males of some species, nervous ganglia have been observed in the neighbourhood of the sac of the spicula.* Organs of sense are not certainly

* The question of the structure and disposition of the nervous system in the *Nematoidea* is, perhaps, not even yet completely

known to exist, unless the pigmented spots on the nervous ring of some free Nematoids have this character.

The *Nematoidea* are for the most part diœcious. In the females, the reproductive aperture is usually placed towards the centre of the body; in the males, it is always situated at or near the posterior extremity.

The female apparatus (Fig. 155, III.) consists of a vagina, with which is connected a single, or double, elongated, tubular, organ, which tapers to a point at its blind extremity, and is at once ovarium, oviduct, and uterus. The cæcal end is occupied by a nucleated protoplasmic mass. Further on, this mass becomes differentiated into an axile cord of protoplasmic substance—the *rhachis*—and peripheral masses, each containing a nucleus and connected by a stalk with the *rhachis*, which are the developing ova. Still further on, in the oviducal portion of the tube, the ova become free; while, in the uterine portion, they are impregnated, and acquire a hard, often ornamented, shell.

The testis is, generally, a single cæcal tube, in the blind end of which cells are developed, much in the same way as in the ovary: they become free in that part of the tube which plays the part of a vas deferens. Contrary to what happens in most animals, these spermatozoa retain the character of cells, and may even exhibit amœboid movements. The deferential end of the testicular tube opens into a sac close to the anus, from the dorsal wall of which one or two curved chitinous spicula are developed. These are introduced into the vulva of the female when copulation takes place, and appear to distend it, in order to allow of the free passage of the seminal corpuscles into the vagina, and thence into the uterus. In the female organs, the seminal cells undergo further changes, and eventually enter into, and coalesce with, the substance of the ova.

Yelk-division follows impregnation. The oval morula

decided; but there is much evidence in favour of what is here stated. See Leuckart, 'Die Menschlichen Parasiten;' the monograph of Schneider, cited below; and especially Bütschli, "Beiträge zur Kenntniss des Nervensystems der Nematoden." ('Archiv für Mikr. Anatomie,' 1873.)

becomes indented on one side, and the embryo, as it grows, folds itself in accordance with this indentation. In most, it would appear that the central cells of the solid morula are differentiated from the rest to form the endoderm, which thus arises by delamination. But Bütschli * has recently shown that the morula, which results from the division of the vitellus of *Cucullanus elegans*, has the form of a flattened plate, composed of two layers of blastomeres, the blastocœle being reduced to a mere fissure. The lamellar blastoderm next becomes concave on one side, convex on the other, and passes into the gastrula form. The blastopore, at first very wide, gradually narrows and appears to be converted into the oral opening of the worm. The mesoblast takes its origin from certain cells of the hypoblast, which lie close to the mouth, and grow thence towards the caudal extremity. The resemblance of this developmental process to that of *Lumbricus* is obvious.

The female reproductive apparatus is, at first, represented by a solid cellular body which lies in the mesoderm; though whether it originally belongs to this, or to the ectoderm, or to the endoderm, is not clear. The cellular body acquires a tubular form, and eventually opens externally by uniting with an inward process of the ectoderm, which gives rise to the vagina.

The young cast their cuticle twice—first, when they leave the egg, and, again, when they acquire their sexual organs.

The *Nematoidea* have been divided into three principal groups †—*Polymyaria*, *Meromyaria*, and *Holomyaria*—characterised by the nature of their muscular system.

* "Zur Entwickelungsgeschichte des *Cucullanus elegans*." ('Zeitschrift für Zoologie,' 1876.) Hallez ('Revue des Sciences Naturelles,' 1877) has observed a similar process in *Anguillula aceti*, but he denies that the blastopore becomes the mouth.

† Schneider, 'Monographie der Nematoden,' 1866. See also Bastian, 'Monograph of the Anguillulidæ' (Trans. Linnean Society, 1865); and 'On the Anatomy and Physiology of the Nematoids' (Phil. Trans. 1866); and several memoirs by Bütschli. The latter affirms that the muscles are as much made up of muscle cells in the '*Holomydria*,' as in the rest. ("Giebt es Holomyarier?" 'Zeitschrift für Wiss. Zoologie,' 1873.)

In the *Polymyaria*, the muscles of the parietes of the body are divided into many series, each made up of many "muscle cells." In the *Meromyaria* there are only eight longitudinal series of such muscle cells, two between each lateral area and the dorsal and ventral lines respectively. In the *Holomyaria* the muscles are not divided into series of muscle cells.

The first two divisions contain only such genera as answer to the general description just given; but, in the *Holomyaria*, there are included several aberrant forms. Thus, *Trichocephalus* has no lateral areas; *Ichthyonema* has no anus; *Mermis* has no anus and the alimentary canal is rudimentary; though it possesses the lateral areas, and the males have spicula. *Gordius* has no lateral areas, and only the ventral line; the alimentary canal is reduced to a rudiment, without either oral or anal aperture, and the male has no spicula. In both these genera, the anterior ends of the embryos are provided with spines, which aid them to bore their way into the bodies of the insects on which they are parasitic. In *Sphærularia* the alimentary canal is similarly rudimentary, and Sir John Lubbock discovered that the small male becomes permanently adherent to the female.

Some *Nematoidea* (*e.g. Leptodera, Pelodera*) live in water or damp earth, and are never actually parasitic; but they require abundant nitrogenous food in order to develope their sexual organs, and hence they are found in the sexual state only among putrefying vegetable or animal matters. The sexless worms, which live in moist earth, are at once attracted by nutriment, such as a few drops of milk.* Here they multiply with great rapidity as long as the store of food lasts; but, when it is exhausted, the last hatched young wander away. In the course of their wanderings, the embryos enter into the larval condition; but, before doing so, they become twice as large as those which attain the larval state in putrefying substances. The embryonic cuticle becomes thickened, and its oral and anal apertures closed, so that it forms a cyst for the larva. The larva, however, is not restrained by this cyst from moving about

* Schneider, *l. c.* pp. 362–3.

and continuing its wanderings, though, at length, it passes into a quiescent condition. Its inner substance, at the same time, becomes dark by transmitted light, in consequence of the accumulation of small fatty granules; and, if this state of things lasts long, the larva dies. If the larvæ should dry up, the circumstance tends to their preservation. The embryonic cuticle is separated, and forms a protective cyst; and, when moistened, the larvæ resume their vital activity.

Nematoid worms belonging to naturally free and non-parasitic genera may enter, and become encysted in, worms and slugs; but they only attain their sexual state when their host dies, and they are nourished by the products of its putrefaction.

Anguillula scandens, the Nematoid which infests and gives rise to a diseased condition of the ears of wheat, is a true parasite. The young are hatched from the eggs laid by the parent in the infected ear, and there become encysted. When the wheat dies down, the larvæ are set free, and wander on the moist earth, until they meet with young wheat plants, up which they creep, and lodge themselves in the developing ears. Here they acquire the sexual condition, nourishing themselves at the expense of the inflorescence, which becomes modified into a kind of gall.

Most Nematoids found in the alimentary canal of animals are parasitic in the sexual state, but have a longer or shorter period of freedom as larvæ or as eggs. But some, as *Cucullanus elegans*, are parasitic both in the sexless and the sexual condition; inhabiting *Cyclops*, while in the former state, and sundry fresh-water fishes, particularly the Perch, in the latter.

Trichina spiralis * acquires its sexual state in the alimentary canal of Man, of the Pig, and other mammals; but the young, set free in the alimentary canal, bore their way through its walls, and enter the fibres of the voluntary muscles, in which they become encysted in the sexless state. If the flesh thus trichinised be eaten, the *Trichinæ*

* Leuckart, 'Untersuchungen über *Trichina spiralis*,' 1866.

are set free, acquire their sexual state in the alimentary canal, and the thousands of embryos which are developed immediately bore their way into the extra-alimentary tissues of their host.

The insect parasites, *Gordius* and *Mermis*, are sexless so long as they are parasitic; but, when they have attained their full growth, they leave the body of their host, acquire sexual organs, copulate, and lay eggs. From these, embryos proceed, which bore their way into the bodies of insects.

It has been stated that the *Nematoidea* are, for the most part, diœcious. Schneider has, however, discovered certain species of the non-parasitic genera, *Leptodera* and *Pelodera*, which always have the external appearance of females, but in the ovarian tubes of which spermatozoa are developed, and impregnation takes place. This was placed beyond doubt by isolating embryos of these Nematoids, and tracing out the development of the spermatozoa, which result from the subdivision of the first cells developed from the rhachis. After a time, the development of spermatozoa ceases, and the cells separated from the rhachis become ova, which are impregnated by the already formed spermatozoa. These *Nematoidea* are probably the most complete and necessary hermaphrodites known in the animal kingdom.

Ascaris nigrovenosa is parasitic in the lungs of Frogs and Toads, and attains a length of three-quarters of an inch. It has the characters of a female, and no male has ever been met with, but spermatozoa are developed in the ovaries in the same manner as in the preceding forms.

The eggs of this *Ascaris* are discharged, and the embryos find their way into the intestines of the Amphibian in which they are parasitic. Here they become males and females which are very much smaller than the hermaphrodite form, (not exceeding one-twentieth of an inch in length) and otherwise different from it. They are evacuated with the fæces of the frog, and passing into damp earth or mud, the females give rise to a few eggs. Embryos are developed from these eggs within the body of the mother, the organs of which they destroy, until her cuticle forms a mere case for them.

The free embryos, introduced into the frog's mouth, pass into the lungs, and take on the characters of the large hermaphrodite forms. It is not unlikely that the Guinea worm (*Filaria medinensis*), which infests the integument of Man in hot climates, may answer to the hermaphrodite stage of a similarly dimorphous Nematoid, though its multiplication has hitherto been supposed to take place agamogenetically.

The many points of resemblance between the *Nematoidea*, the *Oligochæta*, and the *Polychæta* have been indicated by Schneider. They differ, however, from these, no less than from the *Turbellaria* and *Rotifera*, in possessing only longitudinal parietal muscles. In this respect they agree with *Rhamphogordius* and *Polygordius* (united by Schneider into the group of *Gymnotoma*),* which are segmented worms, devoid of setæ, but possessing mesenteries, segmental organs, and pseud-hæmal vessels. *Polygordius* has a telotrochous larva, and in its development, as in other respects, it is extraordinarily like a polychætous Annelid.

Bütschli,† on the other hand, dwells upon the connexion between the *Nematoidea* and the *Gasterotricha* (see Chap. IV. p. 192) and *Atricha* (*Echinoderes*) which he includes in the group of *Nematorhyncha*, on the one side, and the lower Arthropods, such as the *Tardigrada*, on the other.

The PHYSEMARIA.—Since the completion of the third chapter of this work, Haeckel ‡ has published an account of certain low *Metazoa*, constituting the two genera, *Haliphysema* and *Gastrophysema*, which had previously been confounded, partly, with the Sponges and, partly, with the *Protozoa*.

These are minute marine bodies, having the form of cups with longer or shorter stalks, by which they are attached. The cavity of the cup into which the wide or narrow oral

* See *suprà*, p. 186, *note*.

† "Untersuchungen über freilebende Nematoden und die Gattung *Chætonotus*" ('Zeitschrift f. Wiss. Zoologie,' 1876). See also Ludwig, "Ueber die Ordnung Gastrotricha" (*ibid*).

‡ 'Biologische Studien,' Heft 2, 1877.

opening leads, is either simple (*Haliphysema*) or divided by circular constrictions into two or more communicating chambers (*Gastrophysema*). The wall is composed of two layers, an ectoderm and an endoderm—the latter being formed by a single layer of flagellate cells, like those of sponges; and a series of larger flagellate cells are disposed in a spiral, on the inner face of the endoderm near the mouth. The ectoderm is a syncytium, which attaches foreign bodies, such as sponge spicula or skeletons of *Foraminifera*, to itself, and thus becomes provided with an adventitious skeleton, the nature of which varies in different species, but is constant for each. Reproduction is effected by ova, which are said to be modified cells of the endoderm. In *Gastrophysema*, the endoderm of the innermost chamber alone gives rise to ova. The place of development of the spermatozoa has not been made out.

Yelk division is complete and regular, and gives rise to a vesicular morula (*archiblastula* of Haeckel) each cell of which is provided with a flagellate cilium. A gastrula arises by invagination, but the final stages of development have not been made out.

As Haeckel points out, the *Physemaria* are obviously related, on the one hand to the *Porifera*, and on the other to the *Cœlenterata;* in fact, they very nearly represent the morphological common plan of which these two groups are modifications.

The ACANTHOCEPHALA.—In their sexual state, the parasites which constitute the genus *Echinorhynchus* inhabit the various classes of the *Vertebrata*, while they are found in the *Invertebrata* only in a sexless condition.

The *Echinorhynchus* of the Flounder (Fig. 157), the structure of which may serve as an illustration of that of the group, inhabits the rectum of that fish, which it pierces in such a manner that the anterior extremity or head projects, enclosed within a cyst, upon the peritoneal surface, while the body hangs freely into the cavity of the intestine. Where the worm traverses the wall of the rectum it pre-

sents a much constricted neck (Fig. 157, *f*). It would appear that, eventually, the *Echinorhynchi* completely pass out of the intestine, as they are found enclosed in detached cysts lying in the peritoneal cavity. The anterior extremity of the *Echinorhynchus* is produced into a short cylindrical proboscis, covered with many rows of recurved hooks, and, behind this, it forms a dilatation, in which the integument and the muscular coat are separated by a considerable in-

Fig. 157.

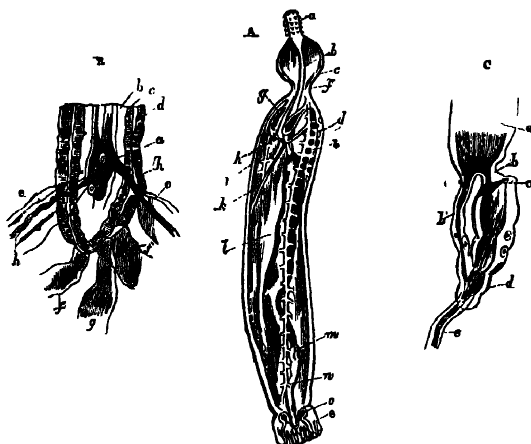


Fig. 157.—*Echinorhynchus*. A. Diagram exhibiting the relative position of the organs. *a*. Proboscis. *b*. Its stem. *c*. Anterior enlargement of the body. *f*. Neck or constriction between the anterior enlargement and the rest of the body, *d*. *e*. Posterior "funnel." *g*. Meniscus. *h*. Superior oblique tubular bands. *k*. Inferior muscles of the proboscis. *l*. *m*. Genitalia. *o*. Penis, or vulva. B. Lower extremity of the stem of the proboscis. *a*. Ganglion. *b*. Vascular space. *d*. Outer coat. *c*. Inner wall. *e*. Tubular band, with the nerve. *h*, *f*. Muscular bands. *g*. Suspensorium of the genitalia. C. Part of the female genitalia. *a*. Ovary. *bb*. Ducts leading from ovary to uterus, spermiducts (?). *c*. Open mouth of oviduct. *d*, *e*. Uterus and vagina.

terval. The body, behind the constricted neck, which separates it from this anterior dilatation, has a thick,

yellowish, outer wall, between which and the inner muscular tunic lies a system of vessels, consisting of two longitudinal trunks, connected by a network of anastomosing canals.

These canals do not appear to possess distinct walls, nor are any cilia visible in them; but the minute molecules which float in the clear fluid which they contain, are driven to and fro, apparently by the contraction of the body. Inferiorly, the vessels all terminate in blind canals, disposed around the margin of the posterior funnel. Internal to the vessels lies a double layer of anastomosing muscular fibrils, the external of which are circular, while the internal are longitudinal.* The cavity of the body is filled with a fluid, in which the ova, or spermatozoa, float, and, at its anterior extremity, two elongated oval bodies depend from the parietes, and hang freely in it. These are the *lemnisci*; they are traversed by vessels continuous with those of the parietes. The axis of the proboscis is continued downwards into an elongated subcylindrical stem, rounded below, which hangs down like a handle into the cavity of the body. The extremity of the stem is connected by broad retractor muscles with the parietes, and gives attachment to the suspensory ligament of the reproductive apparatus (Fig. 157, B). Two other bands are attached a little above these, and run obliquely forwards to the parietes; they are not mere muscles, as they are ordinarily described, but contain a wide vessel, continuous with a large sinus, which separates the axile portion of the stem of the proboscis from its investing coat. In the axis of the stem of the proboscis is the oval ganglion, which sends off some small branches upwards, and two larger lateral trunks, which can be followed into the vessels of the oblique bands; and, in other species, have been traced to the walls of the body and to the genital openings. Two ganglia have been found by Schneider in this region, in the males.

There is no mouth or alimentary canal in *Echinorhynchus*,

* See for an account of the remarkable structure of these muscles, Schneider, "Ueber den Bau der Acanthocephalen." ('Archiv für Anatomie,' 1868.)

the animal being probably nourished by imbibition through the walls of the body. The reproductive organs are, both in the male and in the female, attached by a suspensory ligament to the extremity of the proboscis, and extend thence, through the axis of the body, to the posterior extremity. Here they open in a papilla at the bottom of a funnel-shaped terminal dilatation of the body, which exists both in the male and in the female, though it is much more marked and separated by a constricted neck from the body, in the former. On each side of the papilla is an organ which has much the appearance of a sucker, but which is apparently non-contractile, while the funnel itself undergoes constant and rhythmical contractions.

In the male, the testes are two oval sacs, one behind the other, connected by vasa deferentia, often provided with peculiar accessory glands, with the genital outlet, which is provided with a long penis. In the female, the ovary is a single, long, thin-walled, cylindrical tube, the anterior end of which is usually empty for a short distance. Further back, clear, pale, rounded masses appear, containing cavities in which corpuscles, like the germinal spots of ova, lie. More posteriorly still, these masses become elliptical, and are surrounded by a membranous coat, which gradually thickens, and gives rise at each end to a spiral filament which surrounds the enclosed egg. The ova thus constituted then pass into the cavity of the body, where they accumulate in great numbers; but, in this species, I have not found the free floating ovarian masses described in other *Echinorhynchi*. From the lower end of the ovarium two short oviducts, or rather spermiducts, arise, and almost immediately unite into a sort of uterus, which is continued into the vagina (Fig. 157, C). The uterus passes above into a short, open, funnel-shaped canal, which lies between the two oviducts (Fig. 157, C *c*), and, according to Von Siebold, takes in the ova from the perivisceral cavity by a peculiar swallowing action.

The embryos of the different species of *Echinorhynchi* vary somewhat in structure. Von Siebold has described

those of *E. gigas*, which are provided with hooks disposed like those of the *Cestoidea*, but only four in number. Sexless *Echinorhynchi* have been found in *Cyclops* and in the muscles of fishes. Leuckart states that they acquire sexual organs in the alimentary canal of *Gadus lota*. The same excellent observer has succeeded in tracing the development of *Echinorhynchus proteus*, a common parasite of many river fishes, especially the Perch.* What appeared to be the sexless condition of the same *Echinorhynchus* had previously been seen by Leuckart in *Gammarus pulex*. Into water containing specimens of this Crustacean, ova from *E. proteus* were transferred. After a few days, these ova could easily be detected in the digestive tube of the *Gammarus*, whilst numerous embryos, escaped from the egg-shell, were found within the appendages of the Crustacean.

Each ovum has two coats; an outer, albuminous, and an inner, chitinous. The first is digested in its progress through the alimentary canal; the second is afterwards ruptured by the embryo, which bores through the intestinal walls into the cavity of the body, and is thence conveyed to the site proper for its development.

The body of the embryo is somewhat fusiform in shape, and consists of a colourless, transparent parenchyma, protected by a cuticle. The parenchyma may be resolved into an outer, homogeneous, contractile layer, and a semi-fluid medullary substance. Within this is lodged an ovoid, central mass, made up of large highly-refracting granules. Isolated granules of the same kind may also be found scattered throughout the soft medullary substance. At its posterior end, the embryo tapers to a point, while its opposite extremity is obliquely truncated towards the ventral aspect. On this oblique surface may be observed two series of straight spines, five (rarely six) in each. The two series meet near

* "Ueber Echinorhynchus" ('Göttingen Nachrichten,' 1862). Results of further investigations and a history of the subject are contained in Leuckart's 'Programm,' "De statu et embryonali et larvali Echinorhynchorum eorumque metamorphosi," 1873; and, further, in the concluding part of 'Die Menschlichen Parasiten,' 1876, which has reached me too late for use in this place.

the middle line to form an arch, the central and largest spine constituting its summit. Two short, ridge-like elevations of the cuticle, close to the middle line, separate the spines on either side from one another. Behind, the peripheral layer gives rise to a knob-like process.

At the end of fourteen days, the embryo is found to have increased much in size, but presents few changes of form. The anterior extremity displays two rounded elevations, the spines retaining their original position. The peripheral layer has become thicker and more distinct; its knob-like process has by this time disappeared. The central mass, now much larger, has assumed a spherical figure. No longer granular, it is seen to be composed of numerous pale cells, which continue rapidly to increase.

During the third week, numbers of large yellow granules begin to appear within the outer layer of the embryo. No other changes, save those of growth, take place in its walls: but the central mass, still continuing to enlarge, gradually puts on the aspect of a young *Echinorhynchus*. This mode of development has been compared by Leuckart to that of certain Echinoderms, or to the production of the Nemertid larva within its *pilidium*.

The first part to become differentiated is the cavity of the future proboscis, which appears as a transparent lenticular vesicle at the anterior end of the spherical mass. Behind this are soon seen rudiments of the central axis and its contained ganglion; and the suspensorial ligament, with the reproductive organs, are, at the same time, marked out. The muscles of the outer wall have also commenced their development. Next, the central region of the young *Echinorhynchus* rapidly elongates; its walls become thinner, and, separating from the included structures, show the first trace of the visceral cavity. About this time distinctions of sex first make themselves evident. The posterior end of the body undergoes a disproportionate increase of size, the muscles become more distinct, and the rudimentary generative organs are clearly manifest. At length the young *Echinorhynchus* occupies almost the whole interior

of the embryo, the walls of which have, meanwhile, undergone but slight histological change. The spines, however, have disappeared, together, it would seem, with the cuticle to which they were attached. No rupture of the other embryonic structures takes place, but they gradually attach themselves to the body of the contained *Echinorhynchus*, becoming closely fitted to its surface, and apparently persisting throughout its entire life. The development of the *Echinorhynchus* now approaches completion. The lemnisci appear. Hooks arise on the surface of the proboscis, not, as might be supposed, from its outer cuticle, but from specially modified cells of an inner membrane. The internal organs begin to assume their final aspect. The external form of the adult organism is rather slowly reached, and a few changes which take place after transference of the *Echinorhynchus* to its final host have yet to be observed.

The *Acanthocephala* undoubtedly present certain resemblances to the *Nematoidea*, and more particularly to the *Gordiacea*, but the fundamental differences in the structure of the muscular and nervous systems, and in that of the reproductive organs, are so great, that it is impossible to regard them as Nematoids which have undergone a retrogressive metamorphosis. In their case, as in that of the *Cestoidea* and that of the *Dicyemida*, it is, I think, desirable to keep one's mind open to the possibility that anenterous parasites are not necessarily modifications of free, enterate ancestors.

The DICYEMIDA.—In 1830, Krohn discovered certain ciliated filiform parasites in the renal organs of Cephalopods, to which Kölliker subsequently gave the name of *Dicyema*. Recently, these strange organisms have been made the subject of renewed investigation by E. van Beneden, from whose elaborate memoir * I take the following account of their structure:—

The body of a *Dicyema* (Fig. 158, I.) consists of one large,

* "Recherches sur les Dicyemides." ('Bulletin de l'Acad. Royale de Belgique,' 1876.)

cylindrical, or more or less fusiform, *axial cell*, which extends from the slightly enlarged head-end, by which the animal is attached, to its posterior extremity, and is invested by a single layer of relatively small flattened *cortical*

Fig. 158.

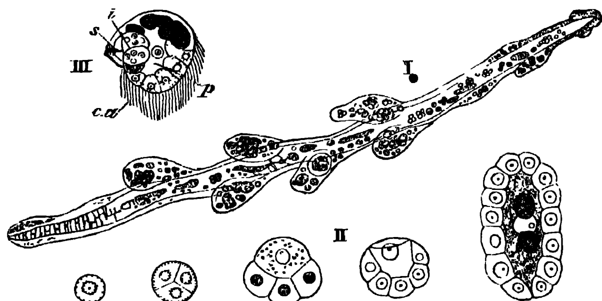


Fig. 158.—*Dicyema.*—I. *D. typus.* The large papillæ of the cortical layer and the germs in the interior of the axial cell are noticeable. II. *D. typus.* Different stages of the development of a vermiform germ. III. Infusoriform embryo found free in the renal organs of *Eledone moschata*, treated with osmic acid: *p*, the urn; *ca*, its capsule; *s*, its lid; *i*, multinucleate cells in its interior. (After Van Beneden, *l. c.*)

cells These are arranged, like a pavement epithelium, around the axial cell, their edges being juxtaposed; they are nucleated, and their free surfaces are ciliated. There is no interspace between the cortical cells and the axial cell, and the organism is a simple cell-aggregate, devoid of connective, muscular, or nervous tissues.

The cortical cells which invest the anterior or head-end of the *Dicyema*, have peculiar characters, and are distinguished as the *polar* cells. They are arranged in such a manner that the head is bilaterally symmetrical. Sometimes the polar cells constitute the whole of the cephalic enlargement, but, in others, cells of the adjacent part of the body (*parapolar cells*) contribute to the investment of

the head. Strongly-refracting globules and rods accumulate in some of the ectodermal cells, and cause them to project in the form of papillæ.

The axial cell is a mass of protoplasm. Its relatively dense outer layer passes into a central reticulation, in the midst of which there is a large oval nucleus.

Reproduction takes place by the formation of germs, and the development of embryos from them, in the axial cell. The embryos are of two kinds, the one vermiform, the other infusoriform, and are not met with in the same *Dicyema*, but in individuals of somewhat different characters. Those which give rise to the vermiform embryos are termed *Nematogena*, while the others are named *Rhombogena*.

In the *Nematogena*, the germs arise in the protoplasmic reticulum of the axial cell, and, at first, are minute spherical bodies, each of which is provided with a nucleus. This germ-cell divides into two, and each of these again becoming bisected, four cells are produced, of which one remains undivided, while the rest go on dividing. The former enlarges, and gives rise to an axial cell, around which the other cells arrange themselves, until eventually they enclose it. Before they meet, they surround an opening through which one end of the axial cell protrudes. This corresponds with the oral pole.

Before the young *Dicyema* thus developed leaves the body, which it generally does by traversing the oral pole, (though it may make its way out through the parietes,) two embryos of the same kind appear within its axial cell.

Thus the nematogenous *Dicyema* gives rise by an agamogenetic process to new *Dicyemas*.

In the *Rhombigena*, the germs are developed in from two to five special nucleated parent cells, the origin of which is not known. They are found imbedded in the protoplasm of the axial cell, and the germs are developed endogenously from the protoplasm of the parent cell, the nucleus of which remains unchanged. The germs undergo division, and become spheroidal bodies composed of two kinds of

cells, small and large. Each of these bodies is converted into an infusoriform, bilaterally symmetrical embryo, which consists of an *urn*, a *ciliated body*, and two *refractive bodies*.

The urn, situated on the ventral side of the embryo, is composed of a *capsule*, a *lid*, and *contents*.

The latter are four granular masses, each of which contains many nuclei, and eventually becomes covered with cilia. The refractive bodies take their origin in two adjacent cells. They partially cover the urn in front, and form the largest portion of the dorsal face of the embryo. The ciliated body consists of ciliated cells, and forms the caudal portion of the embryo.

While the vermiform embryo becomes a *Dicyema* in the body of the Cephalopod on which its parent is parasitic, the infusoriform embryo is set free, and probably serves as the means by which the parasite is transmitted from one Cephalopod to another.

Professor E. van Beneden compares the cortical layer of a *Dicyema* to the ectoderm, and the axial cell to the endoderm of a Metazoon; and the mode of production of the embryo to the process of epiboly in the *Metazoa*. But, from the complete absence of any mesoblastic layer, he proposes to establish a new division of *Mesozoa*, intermediate between the Protozoa and the *Metazoa*, for the *Dicyemida*.

CHAPTER XII.

THE TAXONOMY OF INVERTEBRATED ANIMALS.

The grouping of the various kinds of invertebrated animals which has been adopted in the preceding pages is to be regarded merely as a temporary arrangement. Each chapter, from the second to the tenth, is devoted to a series of forms, the morphological relations of which are more or less obvious, while Chapter XI. is reserved partly for such groups as do not readily find a place in any of the series which precede them; and, partly, for such as have been established since this work was commenced.

Our knowledge of the anatomy, and especially of the development, of the *Invertebrata* is increasing with such prodigious rapidity, that the views of Taxonomists in regard to the proper manner of expressing that knowledge by classification are undergoing, and, for some time to come, are likely to undergo, incessant modifications.

To the beginner, who is apt to make the mistake of looking upon classification as the foundation and essence of morphology, instead of what it really is, the superstructure and outcome thereof, this state of things is distressing. Every handbook presents him with a different system of classification, and he may, not unnaturally, despair of finding any stability in a science, the most general results of which are capable of being stated in such very different ways. If, however, the student will attend to the facts which constitute the subject matter of classifications, rather than to the modes of generalising them which are expressed in taxonomic systems, he will find that, however apparently divergent these systems may be, they have a great deal in common.

It is possible to divide invertebrated animals into a certain number of groups, each of which will be admitted by every morphologist to be in itself a perfectly natural assemblage. That is to say, all the forms thus associated together will resemble one another, and will differ from all other animals, in certain respects. Each such assemblage is, in fact, a "natural order" in the sense in which that word is used by botanists; and, although the number of these natural orders may be increased by the discovery of new forms, or diminished by the ascertainment of closer bonds of union than are at present known to exist, between the orders already discriminated; yet, the morphological types which they represent will always remain; and therefore the knowledge of their characters, once acquired, will be a permanent possession.

It is not needful that these natural orders should be morphologically, still less numerically, equivalent; and, in forming them, it is more important that similarities should not be neglected, than that differences should be overlooked. Those which have been recognized in the preceding pages are enumerated in the following list, arranged in sections corresponding with the chapters in which they are discussed. Under the head of each section, I shall proceed to make such observations as have been suggested to me by new information or by further reflection, during the progress of this work.

Section I.—*Monera* [*Foraminifera*] [*Heliozoa*], *Radiolaria*, *Protoplasta*, *Gregarinidæ*, *Catallacta*, *Infusoria* [*Opalinina*, *Ciliata*, *Flagellata*, *Tentaculifera*].

Section II.—*Porifera*, *Hydrozoa*, *Coralligena* [*Ctenophora*].

Section III.—*Turbellaria*, *Rotifera* [*Nematorhyncha*], *Trematoda*, *Cestoidea*.

Section IV.—*Hirudinea*, *Oligochæta*, *Polychæta*, *Gephyrea*.

Section V.—*Crustacea*, *Arachnida* [*Pycnogonida*, *Tardigrada*, *Pentastomida*], *Myriapoda*, *Insecta*.

Section VI.—*Polyzoa*, *Brachiopoda*, *Lamellibranchiata*, *Odontophora*.

Section VII.—*Echinodermata.*

Section VIII.—*Tunicata.*

Section IX.—*Peripatidea, Myzostomata, Enteropneusta, Chætognatha, Nematoidea, Physemaria, Acanthocephala, Dicyemida.*

SECTION I.—In the commencement of Chapter II., I have expressed a doubt as to the validity of the distinction of the groups contained in this section by the presence or absence of a nucleus, and the recent investigations of Schulze * and Hertwig † have justified my hesitation. These observers have, in fact, demonstrated the existence of one or more nuclei in many *Foraminifera* (*Entosalenia, Polystomella, Rotalia, Textularia,* some *Miliolidæ*). These nuclei may be simple or multiple; in the latter case, they have no special relation to the cameration of the skeleton, and they are single in the young.

The discovery of the nuclei was effected by treating the *Foraminifera* in which they were found in a special manner: and, considering the negative results at which the best observers of the *Foraminifera* have hitherto arrived, and the fact, that the other *Monera* have not been investigated by the same methods, it will probably be wise to consider the question of the non-existence of a nucleus in them as an open one.

Hertwig proposes to include all the Rhizopods which are invested by a coat of chitin, or by silicious or arenaceous particles, or which possess a skeleton, under the head of *Thalamophora*; but the name of *Foraminifera* is now so widely accepted and so long established that I cannot but think that the better course is to retain it.

I have included the *Actinophryida* and the similar forms found in fresh water, and provided with Radiolarian skeletons, with the marine *Radiolaria.*

* "Rhizopoden-Studien, VI." ('Archiv für Mikr. Anatomie,' 1876.)

† "Bemerkungen zur Organisation und systematische Stellung der Foraminiferen." ('Jenaische Zeitschrift,' 1876.)

Hertwig and Lesser,* however, in their important monograph upon the Rhizopods, have stated reasons for separating the former as a distinct group (the *Heliozoa* of Haeckel), though their conclusion that there are, at present, no grounds for assuming even a remote relation between the *Heliozoa* and the *Radiolaria* (l. c. p. 159) appears to me to have no sufficient warranty.

The *Heliozoa* are defined by these authors to be unicellular organisms, which occasionally become multicellular, or at any rate multinucleate, by the multiplication of the nucleus. They are usually spheroidal and free, but some are fixed by means of a stalk. In most, the protoplasm of which they consist is differentiated into a cortical and a medullary substance (ectosarc and endosarc). The sharpness of demarcation of the ectosarc from the endosarc varies. In *Actinophrys sol* the two pass, imperceptibly, one into the other; in *Actinosphœrium*, the change from the ectosarc into the endosarc takes place within a narrow zone, everywhere equidistant from the centre. The line of separation between the endosarc and the ectosarc is best defined in the *Acanthocystidœ*, *Heterophryidœ*, &c., but it arises only from a differentiation of the protoplasm, and not from the development of a definite membranous investment around the endosarc. The nuclei lie in the endosarc. When only one exists it is usually eccentric, and, when there are many, they are scattered irregularly. The ectosarc contains contractile, and sometimes non-contractile, vacuoles, which last may also be met with in the endosarc. The pseudopodia are thin, filiform, and radiate from the body; sometimes their surface presents moving granules. They rarely branch or anastomose. In many cases they present an axial substance which may be traced as far as the endosarc. The silicious skeleton may consist of separate spicula or form a continuous shell.

* "Ueber Rhizopoden und denselben nahestehender Organismen." ('Archiv für Mikr. Anat.,' Bd. X. Supplement heft, 1866.) Full references to the literature of the subject will be found in this memoir and in Dr. Carpenter's 'Introduction to the Study of the Foraminifera,' 1862.

The *Heliozoa* propagate by simple division with or without previous encystation; and the products of division may or may not become encysted. They may either pass directly into the adult state or become monadiform active larvæ, provided with two flagella, a nucleus and contractile vesicle, which in course of time develope into the parent form.*

A completely new light has been thrown upon the vexed question of the supposed sexual method of reproduction of *Infusoria* by the investigations of Engelmann,† Bütschli,‡ and Hertwig,§ the results of whose observations may be summed up as follows:—

1. The so-called acinetiform embryos are parasites.

2. The rod-like bodies occasionally observed in the endoplast are also parasites, and probably *Bacteria*.

3. The globular so-called germs in the *Vorticellidæ* and the bodies termed 'ovules' by Balbiani have nothing to do with reproduction.

* As this chapter was passing through the press, Hertwig's monograph 'Zur Histologie der Radiolarien' has come into my hands. The *Radiolaria* are defined as Rhizopods with pointed, branched, usually anastomosing and granular pseudopodia, which proceed from a protoplasmic body enclosing either numerous small heterogeneous nuclei, or a single larger highly differentiated vesicular nucleus. The protoplasm of the body is further separated into a peripheral non-nucleated and a central nucleated portion, by a membranous capsule with porous walls. The capsule is invested by a homogeneous gelatinous substance; the extracapsular protoplasm usually contains numerous yellow cells.

Propagation is effected (probably always) by the breaking up of the body into unicellular monadiform embryos provided with a single flagellum. As a result of these investigations, Hertwig admits that the *Radiolaria* and the *Heliozoa* are closely allied, and even suggests that the name of *Radiolaria* should apply to both groups, which would then form the subdivisions of *Heliozoa* and *Cytophora*. The *Radiolaria* (*Cytophora*) are distinguished into *Collozoa* (with numerous small nuclei) and *Collida* with a single highly differentiated nucleus.

† "Ueber Entwickelung und Fortpflanzung der Infusorien." ('Morphologisches Jahrbuch,' 1876.)

‡ "Mittheilungen über die Conjugation der Infusorien und die Zelltheilung." ('Zeitschrift für Wiss. Zoologie,' 1875.)

§ "Ueber *Podophrya gemmipara*, nebst Bemerkungen zum Bau und zur systematische Stellung der Acineten." ('Morph. Jahrbuch,' 1876.)

4. In the *Vorticellidæ,* when conjugation takes place, the endoplasts of both individuals break up into a number of fragments. These become mixed up in the common body which results from conjugation. The endoplast of the latter results from the gradual union of many smaller particles which make their appearance in the endosarc. Whether they are identical with the fragments into which the endoplasts of the conjugated individuals have divided, is not certain.

5. When *Infusoria* which possess an endoplastule, as well as an endoplast, conjugate, both of these structures undergo division; and the endoplastule, before division, acquires the striated structure and spindle shape, which has obtained for it the name of 'seminal capsule.'

6. The final result of conjugation is the appearance in each of the individuals which have undergone conjugation of the endoplast and endoplastule (either single or multiple) which characterise the species.

It does not appear that there is any positive proof that the striated endoplastule, or endoplastules, of the conjugated individuals are or are not exchanged. From Butschli's observations on *Stylonichia mytilus,* he concludes that the endoplast divides into four fragments; that these round themselves off into the so-called 'ovules' of Balbiani, and are expelled from the body; while, of the four striated endoplastules into which the endoplastules which exist before fecundation divide, one is converted into a large transparent body, and, dividing, gives rise to the two new endoplasts which appear in the *Stylonichiæ,* after their separation. Two of the others become the new endoplastules; while one, apparently undergoing retrogressive metamorphosis, is cast out of the body.

From these facts, and from the circumstance that the endoplastules of *Infusoria,* which are merely dividing, acquire the striated structure, it must be concluded that the ascription of a spermatozoal nature to the striæ of the modified endoplastules is not warranted. And the remarkable ob-

servations of Butschli, Strassburger,* Van Beneden and Hertwig,† on the changes which take place in the nuclei of both animal and vegetable cells, which are undergoing division, or are preparing for fecundation, seem to leave no doubt as to the justice of this negative conclusion. In such cells the nucleus becomes elongated and assumes a striated appearance, so as to resemble in a very striking manner, the so-called 'seminal capsule' of the Infusoria. Nevertheless, it is still possible that the conjugation of the *Infusoria* may be a true sexual process; and that a portion of the divided endoplastules of each may play the part of the spermatic corpuscle; the conjugation of which with the nucleus of the ovum, appears, from recent researches, to constitute the essence of the act of impregnation.

With the proof that the 'acinetiform embryos' of the *Infusoria ciliata* are parasites, the view of the relations of the *Tentaculifera* with the *Ciliata*, suggested at p. 109, ceases to be exactly tenable. Nevertheless the resemblance of the ciliated young *Acinetæ* to the simpler forms of the *Ciliata* is so close that they may still be said to be modifications of a common type. Hertwig ‡ has made the interesting observation that, in some *Acinetæ*, the tentacula are of two kinds; those of the one kind are the characteristic suctorial organs, while those of the other kind are simply prehensile, and have a structure very similar to that of the prehensile pseudopodia of the *Actinophryidæ*. The same author shows that the ciliated germs do not arise from the endoplast alone, but that a portion of the protoplasm of the body invests each division of the endoplast. In fact the process by which these germs are developed is altogether similar to ordinary cell-division.

The *Opalinina* must clearly be arranged among the

* 'Ueber Zellbildung und Zelltheilung,' 1876.

† "Beiträge zur Kenntniss und Bildung, Befruchtung und Theilung des thierrischen Eies." ('Morph. Jahrbuch,' 1876.)

‡ "Ueber *Podophrya gemmipara* nebst Bemerkungen zum Bau und zur systematische Stellung der Acineten." ('Morphologisches Jahrbuch,' 1876.)

Infusoria. Stein regards them as simply the lowest forms of the *Holotricha,* but it will probably be safer to consider them as a distinct group, standing in somewhat the same relation to the *Ciliata* as the *Gregarinidæ* do to the *Amœbæ.*

SECTION II.—The elucidation of the problem of the mode of development of the Sponges has been greatly advanced by the investigations of Oscar Schmidt,* Schulze,† and especially of Barrois,‡ which confirm the assertion of Metschnikoff that the vesicular morula which constitutes the early condition of the sponge-embryo consists of blastomeres of two kinds; those of the one half of the spheroidal or flattened embryo being elongated and flagellate; those of the other, rounded, granular and non-ciliated. Schulze and Barrois have independently ascertained that the latter region sometimes undergoes partial invagination; and that a cup-shaped body is produced, composed of an epiblast formed of flagellate cells and a hypoblast of spheroidal, non-ciliated cells. Thus the "gastrula" stage of Haeckel may exist, though it is not formed by delamination, as he supposed, but by invagination. But it appears that this gastrula-stage does not always occur, and that when it does, it is transitory, in so far as the hypoblastic cells subsequently enlarge, protrude beyond the epiblastic cells, and give rise to the free ovate embryo formed of a ciliated and non-ciliated half, which has so often been observed. According to Barrois' observations, this free swimming larva fixes itself by its non-ciliated hypoblastic half, and the hypoblastic cells are invested by those of the epiblast, which thus constitute the whole outer covering of the young sponge. The central cavity of the sponge, which represents the archenteron, arises in the midst of the included hypo-

* 'Zur Orientirung über die Entwickelung der Spongien" ('Zeitschrift für Wiss. Zoologie,' 1875); and "Nochmals die Gastrula der Kalkschwämme" ('Archiv f. Mikr. Anat.,' 1876).

† "Ueber den Bau und die Entwickelung von *Sycandra raphanus*" ('Zeitschrift f. Wiss. Zoologie,' 1875); and "Zur Entwickelungsgeschichte von Sycandra" (Ibid. 1876.)

‡ 'Annales des Sciences Naturelles,' 1876.

blastic cells, while the osculum is a secondary opening, formed apparently by an invagination of the ectoderm, and has nothing to do with the primitive blastopore. Thus even the simplest sponge has passed beyond the gastrula-stage.

Schulze has made the important discovery that, in *Sycandra raphanus*, there is a layer of flattened cells external to the syncytium; whence the latter may rather be regarded as the equivalent of the mesoderm than of the ectoderm of the *Cœlenterata*. And the observations of Barrois on other calcareous sponges tend to the same conclusion. The careful investigations of the last-named writer have not enabled him to discover spermatozoa in any sponge, and he finds that the ova, when they are first discernible, are situated in the syncytium or mesoderm, and not in the endoderm. In the free larvæ of the calcareous sponges an equatorial zone of rounded equal-sized blastomeres is interposed between the ciliated, or epiblastic, and the non-ciliated, or hypoblastic, hemisphere; and it appears probable that these cells represent a mesoblast and give origin to the mesoderm. The embryo in this condition has a very interesting resemblance to that of *Clepsine*, in the stage in which the epiblast occupies one face of the embryo, and the hypoblast, formed of three very large blastomeres, the opposite face; while an incomplete zone of six or eight large blastomeres, which are eventually enclosed by the epiblast, surrounds the margins of the latter.

At p. 150, I have quoted Haeckel's account of a process of *Entogastric* gemmation in *Carmarina hastata* of an altogether anomalous character.

F. E. Schulze* has lately investigated specimens of *Geryonia hexaphylla* provided with entogastric processes beset with budding *Cuninæ*, and he proves that, in this case, at any rate, the phenomenon is one of parasitism.

* "Ueber die Cuninen Knospenaehren im Magen v. Geryonien." ('Mittheilungen des Naturwissenschaftlichen Vereines.' Graz, 1875.)

The stem from which the buds proceed, in fact, is not a process of the body of the *Geryonia*, but is simply attached to the wall of the gastric chamber of the latter. It is hollow, and its cavity is lined by an endodermal epithelium. The *Cunina* buds are not developed from the epithelium which covers the stem and represents its ectoderm, but commence in the ordinary way, as cæcal diverticula of the wall of the stem, the apices of which soon open to form the hydranth of a medusoid, the disk of which results from the outgrowth of the base of the hydranth. In all probability the larva of the *Cunina* enters the gastric cavity of the *Geryonia* as a planula; and, attaching itself to the wall, grows out into a stolon whence the medusoids bud.

It may be suspected that the other cases of supposed entogastric proliferation will prove to be susceptible of a similar explanation.

Although, as I have endeavoured to show, the *Ctenophora* are readily reducible to the general plan of the *Actinozoa*, yet considering their many peculiar characters, I think it is advisable to separate them from the *Coralligena*, as a distinct natural order.

Moreover, the *Physemaria* must undoubtedly be placed in this section, which will therefore consist of the following natural orders: *Physemaria, Porifera, Hydrozoa, Coralligena, Ctenophora.*

SECTION III.—I concur in the proposal of Bütschli* to establish a group, *Nematorhyncha*, for the genera *Chætonotus*, *Echinoderes*, and their allies, to which reference is made at p. 192. The *Nematorhyncha* are divisible into the *Gastrotricha* † (*Chætonotus, Chætura, Cephalidium, Ichthydium, Turbanella, Hemidasys* and *Dasydites*), which are ciliated on the ventral surface of the body, and the *Atricha* (*Echinoderes*), which possess no cilia. Bütschli finds two

* "Untersuchungen über freilebende Nematoden und die Gattung *Chætonotus*." ('Zeitschrift für Wiss. Zoologie,' 1876.)

† See H. Ludwig, "Ueber die Ordnung Gastrotricha.' ('Zeitschrift für Wiss. Zoologie,' 1876.)

convoluted water-vessels analogous to those of the *Rotifera*, but apparently not ciliated, in *Chætonotus*.

SECTION IV.—Our knowledge of the development of the *Hirudinea* has received an important addition in the 'Mémoire sur le développement embryogénique des Hirudinées,' by M. C. Robin; who, among other important contributions to embryology, has rectified some important errors of Rathke respecting the early stages of the development of *Clepsine*. I have found the description and figures of the various stages of cleavage, and of the steps by which the blastoderm is converted into the young *Clepsine*, given in this memoir, to be exceedingly accurate.

The whole process in *Clepsine* is very similar to that which has been described in *Euaxes* by Kowalewsky* and shares with it the remarkable peculiarity that the first formed portion of the blastoderm becomes the hæmal region of the body. As this blastodermic disk grows, its margins thicken and give rise to two germ-bands (Keimstreifen). These gradually approximate and eventually unite upon the opposite face of the ovum. As the chain of ganglia is the product of the differentiation of the epiblast of the germ bands, it follows that it is formed by the union of two primarily distinct nerve tracts, which move round from the hæmal to the neural aspect of the body; and thus the arrangement of the nervous trunks in *Malacobdella* † may be regarded as expressive of a condition which is transitory in *Clepsine* and *Euaxes*.

* 'Embryologische Studien an Würmern und Arthropoden.' ('Mém. de l'Acad. Imp. de St. Pétersbourg,' 1871.)

† According to Semper's recently published statements, *Malacobdella* is a true Nematoid, and not a Leech. ("Die Verwandtschaftsbeziehungen der gegliederten Thiere," 'Arbeiten aus d. Zoologisch-Zootomischen Institut in Würzburg,' Bd. iii., 1876.) The memoir here cited is full of important observations respecting the structure of the nervous system in the *Annelida*; the agamogenetic multiplication of *Nais* and *Chætogaster*; and the development of the organs of these Annelids.

Moreover, the author discusses very fully the relation of the Annelidan with the vertebrate types of organisation. I do not propose to touch upon this subject in the present volume; but I

Many years ago* I directed attention to the fact that "the development of a Mollusk commences on the hæmal side and spreads round to the neural side, thus reversing the process in Articulata and Vertebrata;" and it is very interesting, considering the many curious points of approximation between the *Annelida* and the *Mollusca* which are now coming to light, to observe that certain Annelids present this especially Molluscan peculiarity.† As Von Baer long ago pointed out, there is a striking likeness between the foot of a Gasteropod and the suctorial disk of one of the *Hirudinea*. The so-called jaws of the Leeches (the 'teeth' of which, I may observe in passing, are calcified) are curiously similar to an odontophore devoid of cartilages, the representative of the radula being supported on a muscular cushion.

The statement at p. 245, that "no calcareous skeleton is found in any of the *Gephyrea*" ceases to be true since the discovery of L. Graff,‡ that the minute spines of *Chætoderma* are calcified. It is a further peculiarity of this genus, that two distinct nerve cords proceed from the cerebral ganglia, parallel with one another, on each side of the body, in the place of the single median nerve cord of other members of the group.

Dr. Jhering § has directed attention to certain points of

may remark that the evidence upon which the identification of the structures termed "Kiemengangwülste" and their products with the branchial apparatus of vertebrate animals is founded, appears to me to be wholly inadequate to bear out the conclusions deduced from it.

* 'On the Morphology of the Cephalous Mollusca.' ('Phil. Trans.,' 1852, p. 45 and *note*.)

† The mode of development of the central nervous system in *Euaxes* and *Clepsine* offers many points of interest. Not the least important of them is the obvious similarity (to which attention has already been directed by Semper) between the germ bands of *Clepsine* when they have united throughout the greater part of their length, but surround the blastopore behind, and the Amphibian embryo with its dorsal ridges, which have exactly similar relations (See for example Fig. 40, in Plate III. of Götte's work 'Die Entwickelungsgeschichte der Unke.')

‡ "Anatomie des *Chætoderma nitidulum*." ('Zeitschrift f. Wiss. Zoologie,' 1876.)

§ 'Vergleichende Anatomie des Nervensystems der Mollusken,' 1877.

There is no invertebrated animal at present known, which cannot at once be referred to one or other of the natural orders which have been discussed in the preceding pages. The next question which arises is, how far are these groups susceptible of arrangement into assemblages of a higher order, distinguished from all others by certain common characters?

It is universally admitted that the *Insecta, Myriapoda, Arachnida, Crustacea, Pycnogonida*, and *Tardigrada*, form such an assemblage, termed the ARTHROPODA, and characterised by the segmentation of the body; the chitinous cuticula; the absence of cilia upon, or in, the body at any period of life; the segmentation of the central nervous system and its perforation by the gullet: and the presence (with the possible exception of the *Trilobita*) of limbs, which, almost always, are themselves subdivided into joints. The reasons for including the *Peripatidea* in this division have been given in Chap. XI.; and though the *Pentastomida* must be regarded as hardly within the limits of the definition, I think that, taking into account the strange modifications which are undergone by the parasitic *Crustacea* and *Arachnida*, it is not needful to depart from the ordinary practice of associating them with the *Arthropoda*.

The *Lamellibranchiata* and the *Odontophora* constitute another very well marked division, the MOLLUSCA, the characters of which have been discussed in Chapter VIII.

The proposal to separate the *Polyplacophora* from the *Mollusca*, to which I have already referred, appears to me to be devoid of any justification. The resemblances between certain *Gephyrea*, such as *Chætoderma* and *Neomenia*, and the *Polyplacophora*, are accompanied by wide differences;

Jhering. Nevertheless I may remark that, had he condescended to pay attention to what is said respecting the flexure of the intestine in Mollusks in that antiquated production, he would not have committed himself to the publication of the two diagrams, one of a Cephalopod and the other of a Pteropod, each with its alimentary canal twisted after a fashion of which nature knows nothing, which illustrate, though they hardly adorn, page 272 of his work.

and even if these resemblances are to be regarded as evidences of affinity, some considerations, such as the restriction of the branchiæ to the hinder part of the body, and the reduction of the foot in *Chitonellus*, rather lead to the suggestion, that *Chætoderma* and *Neomenia* may be extremely modified Mollusks, allied to the *Polyplacophora*.

As to the supposition that the resemblances between the *Nudibranchiata* and the *Turbellaria* indicate a direct affinity between these groups, it seems to be forgotten that the *Nudibranchiata* are all, when young, unmistakeable Gasteropods provided with mantle and shell. Their adult structure is as little evidence of any Turbellarian affinities as that of *Lernœa* is proof of its being allied to the worms, rather than to the *Crustacea*.

The *Physemaria*, the *Porifera*, the *Hydrozoa*, the *Coralligena* and the *Ctenophora* are obviously modifications of the same fundamental plan. I think it is convenient to retain the well-established name of *Cœlenterata* for the last three orders, which are much more closely related to one another than to the other two. Haeckel's proposal to apply the old name of ZOOPHYTA to the whole division appears to me to be well worthy of adoption. The inconvenience of using a term the connotations of which have varied somewhat widely since it was first invented, is probably less than that which would attend the invention of a new name.

The *Monera*, *Foraminifera*, *Heliozoa*, *Radiolaria*, *Protoplasta*, *Gregarinida*, *Catallacta* and *Infusoria*, (*Opalinina*, *Ciliata*, *Tentaculifera*, *Flagellata*), again, are so closely united together that the difficulty is to distinguish the less differentiated forms of each from one another. They constitute the division of the PROTOZOA, the common characters of which have been given in Chapter II.

If there were no invertebrated animals beside those included under these four divisions of ARTHROPODA, MOLLUSCA, ZOOPHYTA, and PROTOZOA, the task of classification would be very easy, and each of the higher divisions

would be sharply defined from the others. But a vast residuum remains to be considered; and it is with the attempt to arrange these residual orders into higher groups that the difficulties of the Taxonomist commence.

The *Polychæta* and the *Oligochæta*, the *Hirudinea* and the *Gephyrea*, resemble one another generally in the segmentation of the body, indicated at least by the serially multi-gangliate nervous centres;* in the presence of cilia and of segmental organs; and in the nature of the larvæ which are set free, when their embryos are hatched in an early stage of development. And although no one of these characters is of universal occurrence (cilia, for example, being absent in most adult *Hirudinea*), yet they are found in such association, that the accepted arrangement of these four groups (to which, though not without some hesitation, I add the *Myzostomata*), into the division of the ANNELIDA, is undoubtedly very convenient.

The *Trematoda*, the *Turbellaria*, and the *Rotifera*, form another very natural assemblage. But it must be admitted that the highest forms of this division are separated by no very sharp line of demarcation from the *Annelida*; while the simplest *Turbellaria* are almost on a level with the *Physemaria* and the lower *Hydrozoa*. Even a *Planaria* is comparable to a free zoophyte; its proboscis may be likened to the hydranth of a *Medusa*, the prolongation of the alimentary sac to the gastro-vascular canals, the central nervous system, with its lateral prolongations, to the marginal ganglia and nerves. The water-vascular system and the complication of the reproductive organs, indeed, afford clear marks of distinction; but both of these systems vary indefinitely in the degree of their development within the limits of the *Turbellaria*.

On the other hand, the connection of the *Hirudinea*, by such forms as *Malacobdella* with the *Turbellaria* and *Trematoda* is very close; *Polygordius* appears to be a transitional

* This character is wanting in most *Gephyrea*, which, as I have remarked at p. 248, incline in many respects towards the next division, and especially toward the *Rotifera* and *Nematorhyncha*.

form between the *Turbellaria* and the *Polychæta*; while the *Rotifera*, in many respects, represent larval forms of the *Polychæta* and of the *Gephyrea*.

The *Cestoidea* are usually regarded as anenterous *Trematoda*, in which case, of course, they must be associated with the latter.

I propose to establish a division of TRICHOSCOLICES for the natural orders now enumerated, in order to discriminate the morphological type which they exemplify from that of the NEMATOSCOLICES, containing the *Nematoidea*, which are as remarkable for the universal absence of cilia as the former are for their presence; and which are further so clearly distinguished by the arrangement of their nervous and muscular systems and of their water-vessels; and by their ecdysis.

The connexion between the two divisions by way of the *Nematorhyncha* and the *Rotifera* is undoubtedly very intimate, and there is almost as much reason to arrange the *Nematorhyncha* with the *Trichoscolices*, as with the *Nematoscolices*. On the whole, however, I think that, notwithstanding the cilia of the *Gastrotricha*, the closest affinities of the *Nematorhyncha* are with the *Nematoidea*, and I therefore place them among the *Nematoscolices*.

But I may remark once for all, that the attempt to establish sharply defined large divisions of the animal kingdom is futile. The progress of knowledge every day renders it more and more clear, that morphological groups are comparable to distributional provinces; each, however well marked may be its characteristic features, shades off at its margins into some other group; and the object of classification is simply to bring into prominence the morphological types which embody these characteristic features.

It appears to me impossible to compare the structure and the larval conditions of a Polyzoon with those of a Brachiopod, without arriving at the conclusion that they are more closely allied with one another than they are with

any third group. Nevertheless, the *Polyzoa* approach the *Rotifera*, and the *Brachiopoda*, the *Annelida*, on the one side; while, on the other, they present unmistakeable affinities with the lower *Mollusca*. At the same time, the weight of the resemblances between the *Polyzoa* and the *Tunicata*, which led Milne-Edwards to the establishment of the group of "Molluscoïdes" (adopted by myself under the title of *Molluscoida*) has been much lessened by the progress of investigation.

I conceive that we may best keep these resemblances and differences in view by associating the *Polyzoa* and the *Brachiopoda* into a division apart, for which I propose the name of MALACOSCOLICES; in order to indicate its relations with the Worms on the one side, and with the *Mollusca* on the other.

The *Tunicata* are absolutely distinguished from all other invertebrated animals except *Balanoglossus*, by the perforation of the pharynx and its conversion into a respiratory organ.*

At first sight there appears to be little ground for the approximation of groups apparently so widely different as the *Tunicata* and the *Enteropneusta*. But the extraordinary similarity in the structure of the perforated pharyngeal sac in the larvæ of Tunicates and of *Balanoglossus*, is a fact of great morphological weight. An ecaudate *Appendicularia* of those species which have the alimentary canal nearly straight, would be marvellously like a larval *Balanoglossus*, which is again little more than a specially modified Turbellarian. I think, therefore, that the *Tunicata* and the *Enteropneusta* may properly constitute a division of PHARYNGOPNEUSTA.

The Tunicate *Pharyngopneusta*, with their caudate larvæ may be supposed to stand in the same relation to the

* I have alluded above to the structures described by Semper in some *Oligochæta* and in *Sabella*. I do not doubt the accuracy of the description; but it does not lead me to conclude that the structures in question are homologous with either Vertebrate, Enteropneustal or Tunicate branchiæ.

Turbellariform *Pharyngopneusta*, as the *Trematoda*, with their cercariform larvæ, to the *Turbellaria*.

Another very well marked division is that of the ECHINODERMATA, the characteristics and relations of which have been fully discussed in Chapter IX.

Although the structure and development of *Sagitta* have now been as thoroughly elucidated as those of any animal, the proper Taxonomic place of the *Chætognatha* is still an unsolved problem. The issues, however, appear to be narrowed to these: either they belong to the *Annelida*, or to the *Nematoscolices*, or to the *Trichoscolices*; or the *Chætognatha* are to be regarded as an independent division, allied to all these, and perhaps to the lower *Arthropoda*. I am disposed to adopt the last view, chiefly on the ground of the mode of development of *Sagitta*, which is unlike anything at present known to occur in *Annelida*, *Trichoscolices*, *Nematoscolices*, or *Arthropoda*.

The *Acanthocephala* are hardly less anomalous than the *Chætognatha*. Taking into account the *Gordiacea* and the characters of the proboscis in the *Nematorhyncha*, there is undoubtedly room for the suggestion that they are specially modified anenterous *Nematoscolices*, and should be classed among the latter. But here, as in the case of the *Cestoidea*, there are many difficulties in the way of accounting for these anenterous forms by the supposition that they are the results of a retrogressive metamorphosis of enterate animals.

This question of the true relations of the anenterous invertebrates—by which I mean not only those which, like the male Rotifers, have no functional alimentary canal in the adult condition; but those which, like the *Cestoidea* and the *Acanthocephala*, never exhibit a trace of an alimentary canal, even in the embryo; which is usually dealt with so summarily by the assumption of retrogressive metamorphosis, acquires still more importance, when we attempt to determine the Taxonomic place of the *Dicyemida*.

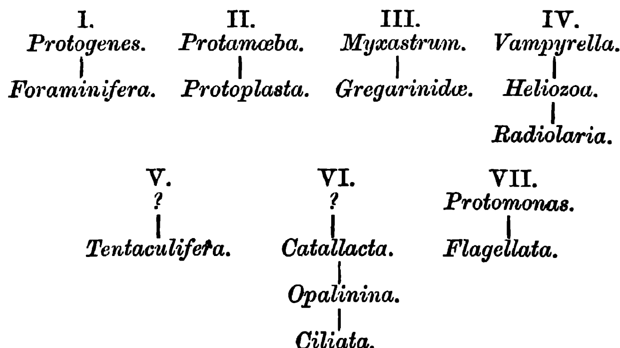
Professor E. van Beneden has proved that these parasites cannot be dismissed, *sans façon*, as retrogressively metamorphosed 'worms;' and though I am not disposed to attach much weight to the absence of a mesoderm, on which Van Beneden insists as a distinction between the *Dicyemida* and the *Metazoa*, the manner in which the contents of the axial cell give rise to germs is so completely unlike anything which is known to obtain in the *Metazoa*, as, to my mind, to justify the separation of the *Dicyemida* from the whole of this division. On the other hand, the similarity of their development to the formation of metazoic embryos by epiboly, as completely divides the *Dicyemida* from all the *Protozoa*. It must be recollected that the changes which are undergone by the ciliated embryos are still to be discovered; but, provisionally, I am disposed to agree with Van Beneden, that the *Dicyemida* should be regarded as the representatives of a distinct division, the MESOZOA, intermediate between the *Protozoa* and the *Metazoa*. And without distinctly pledging myself to any such view, I yet think it is worth while to throw out the suggestion that the *Cestoidea*, if not the *Acanthocephala*, may be modifications of the same type, differing from the *Dicyemida* in the development of a mesoderm, but resembling them in the total absence of an alimentary apparatus.

THE SERIAL RELATIONS OF THE INVERTEBRATA.—When the various groups of invertebrate animals are compared, it is obvious that they present very different degrees of morphological complexity; whence they may be considered as terms in a graduated progression, in which the place of each group corresponds broadly with the degree of its differentiation. The lowest *Protozoa* will occupy one extreme of such a progression, the *Arthropoda* and the *Mollusca*, the other, while the remaining groups fall into intermediate places. On attempting to carry out this serial arrangement into detail, however, it will be found that no single series will suffice to express the facts, but that, starting from the lowest *Protozoa*, we are led along various

lines, none of which, as far as our present knowledge enables us to judge, can be traced, without interruption, throughout the whole length of the scale.

If we assume, in the absence of proof to the contrary, that the *Monera* have the simplicity of structure ascribed to them by Haeckel; then, on comparing the *Endoplastica* with the *Monera*, the different groups of the former appear to be related to those of the latter division, as if they were similar forms complicated by the addition of one or many nuclei. *Protogenes* may thus be considered as the root of the Foraminiferal series, *Protamœba* of the *Protoplasta*, *Myxastrum* of the *Gregarinidæ*, *Vampyrella* of the *Heliozoa*, *Protomonas* of the *Flagellata*. A Moneran, ciliated over its whole surface, which might stand in the same relation to the *Opalinina*, *Catallacta*, *Tentaculifera*, and *Ciliata*, is at present unknown. The *Protozoa* thus fall into the following series:—

PROTOZOA.



I am unable to trace any one of these series of modifications further; that is to say, to find forms which actually bridge over the interval between any one of them and the *Metazoa*, though it is easy enough to imagine what such forms might be. The spheroidal free-swimming monad aggregates, such as *Uvella* and *Polytoma*, and *Magosphæra*

itself, are, in many respects, comparable to Physemarian or Poriferan embryos; while an animal *Volvox* would be a sort of permanent vesicular morula. So, one of the higher *Infusoria*, if it became multinucleate, like an *Opalina*, would approach the lowest *Turbellaria*.

The axial cell of a *Dicyema*, from the protoplasm of which its ciliated and non-ciliated germs are produced, is, to a certain extent, comparable to the capsule of a Radiolarian; while, on the other hand, a Radiolarian with a multinucleate cortical layer would approach the structure of *Dicyema*. And if what is at present known of *Dicyema* gives a just conception of the essential points of its entire history, it undoubtedly, as E. van Beneden has suggested, represents a type intermediate between the *Protozoa* and the *Metazoa*, though it can hardly be said to fill up the *hiatus* between them.

In our further search after the serial relations of animals, we must therefore start afresh from the lowest *Metazoa*. Here a ZOOPHYTIC SERIES is very well marked; commencing with the *Physemaria*, and thence diverging, on the one hand, to the *Porifera*, and, on the other, to the *Cœlenterata*, with the highest forms of which this series comes to an end.

A second gradation, which may be termed the ANNULOID SERIES, is represented by the *Trichoscolices* and the *Annelida*. The lowest *Turbellaria* are upon nearly the same level of organisation as the *Hydrozoa*. It would be hard to distinguish an aproctous Turbellarian, devoid of a ganglion and water-vessels, from a free-swimming non-tentaculate Hydrozoon. On the other hand, as I have already pointed out, the line of demarcation between the higher *Trichoscolices* and the *Annelida* is very indistinct, and we may expect it to be speedily obliterated by the progress of discovery.

A third gradation is constituted by the *Nematoscolices* and the *Arthropoda*. The lowest *Nematoidea* possess no higher organisation than the lowest *Turbellaria* and the *Rotifera*.

The *Nematorhyncha*, whether they are really transitional forms between the *Nematoidea* and the *Arthropoda* or not, at any rate, indicate the road by which the transition may be effected; and I am much inclined to think that the *Chætognatha* may occupy a place in this series. The oral armature of *Sagitta* may be regarded as a modification of the oral spines of *Echinoderes*, and its nervous system is as much Arthropodal as is that of the *Pentastomida*. This may be called the ARTHROZOIC SERIES.

A fourth series is that which I shall term the MALACOZOIC SERIES. It includes the *Malacoscolices* and the *Mollusca*. The entoproctous *Polyzoa* form the lowest term of this series. The resemblances of the *Polyzoa* with the *Rotifera* (*e. g.* with *Stephanoceros*) have often been remarked, and, indeed, insisted upon, with too little regard to the differences which are established by the water-vessels and the peculiar pharyngeal armature of the Rotifers. Nevertheless, these resemblances are important as far as they go, and in grade of organisation the two groups are much upon the same level, On the other hand, the comparison of a Polyzoon with a larval Lamellibranch or Gasteropod, or with a Pteropod, leaves no doubt in my mind that the *Malacoscolices* have the same relation to the *Mollusca*, as the *Trichoscolices* to the *Annelida*.

A fifth gradation is presented by the *Tunicata* and the *Enteropneusta*, which constitute the PHARYNGOPNEUSTAL SERIES. I do not regard the *Enteropneusta* as of distinctly lower organisation than the *Tunicata*, but rather as a collateral group; and I conceive it to be probable that some lower forms, connecting the *Enteropneusta* and the *Tunicata* with one another and with the *Trichoscolices*, will yet be found. However this may be, *Appendicularia* presents a grade of organisation but little higher than that of the *Polyzoa*.

A sixth gradation is represented by the ECHINODERMAL

SERIES. Like the foregoing, this series at present stands isolated,* no annectent forms between the Echinoderms and higher or lower groups being known. On the ground of the uniformity of character of the larvæ of the Echinoderms, however, there can be little doubt that, if ever such forms are discovered, they will prove to be allied to the *Gephyrea*, the *Trichoscolices* and the *Enteropneusta*.

Thus the study of the gradations of structure among the *Metazoa* leads to the conclusion that they fall into six series, which may be arranged in the following tabular shape:—

SERIES.

I.	II.	III.	
ZOOPHYTIC.	ECHINODERMAL.	PHARYNGOPNEUSTAL.	
Cœlenterata.	*Echinodermata.*	*Enteropneusta.*	*Tunicata.*
Porifera.			
Physemaria.			

IV.	V.	VI.
MALACOZOIC.	ANNULOID.	ARTHROZOIC.
Mollusca.	*Annelida.*	*Arthropoda.*
		Chætognatha (?).
Malacoscolices.	*Trichoscolices.*	*Nematoscolices.*

The lowest known term of the Arthrozoic series is a Nematoid worm; that of the Annuloid series is a low Turbellarian or Rotifer; that of the Malacozoic series is an entoproctous Polyzoon; that of the Pharyngopneustal series is probably most nearly exemplified by the young larva of *Balanoglossus;* that of the Echinodermal series by the vermiform *Echinopædium.*

But the differences between one of the simpler Nematoid worms, an aproctous Turbellarian, a Rotifer, an Echinopædium and a *Pedicellina,* are relatively so small, that all six series may be said to converge towards a common

* I say, at present, inasmuch as the characters of the nervous system sharply separate the most vermiform of the Echinoderms from the most Echinoderm-like *Gephyrea.*

form; and that common form, when the special characters of each group are eliminated, and the alimentary canal is reduced to its primitive aproctous condition, would be exceedingly similar to a Physemarian.

Hence the consideration of the gradations of structure which are presented by the various series of Invertebrated animals, irresistibly leads to the conclusion that the whole of the *Metazoa* may be conceived as diverse modifications of a common fundamental plan.

THE SERIAL RELATIONS OF THE INVERTEBRATA COMPARED WITH THE RESULTS OF EMBRYOLOGY.—The conception of the unity of organisation of the *Invertebrata* thus reached, so far as it is based upon the comparison of adult structures, is purely ideal; and the study of the development of individual animals is alone competent to decide the question whether this ideal unity has a foundation in objective fact. But the history of the development of animals appertaining to every group of the *Invertebrata* which has been given, bears out the statement which is made in the Introduction that the ideal unity has such a foundation in fact; inasmuch as all these animals commence their existence under the same form; that namely of a simple protoplasmic body, the ovum or germ.

In the Introduction I have said that "among the lowest forms of animal life, the protoplasmic mass which represents the morphological unit may be, as in the lowest plants, devoid of a nucleus" (p. 12). However, as I have remarked at the commencement of this chapter, until the search for the nucleus has been instituted afresh, with the help of such methods as have recently proved its existence in the *Foraminifera*, I think it will be wise to entertain a doubt whether any of the *Monera* are really devoid of this amount of structural differentiation; and the tendency of recent investigations appears to render it very questionable whether the nucleus of the ovum ever really disappears, whatever may be the modifications undergone by the germinal vesicle and its contents. I shall, therefore, assume provisionally,

that the primary form of every animal is a nucleated protoplasmic body, *cytode*, or *cell*, in the most general acceptation of the latter term.

Whether the primary cytode possesses a nucleus or not, the important fact remains, that in its earliest condition, every invertebrated animal, if it were competent to lead an independent existence, would be classed among the *Protozoa*.

The first change which takes place in the development of the embryo from the primitive cytode, or impregnated ovum, in all the *Metazoa*, is its division; and the simplest form of division results in the formation of a spheroidal or discoidal mass of equal, or sub-equal, derivative *cytodes*, the blastomeres. Next, the *morula*, thus formed, generally acquires a central cavity, the *blastocœle*, and becomes a hollow vesicle, the *blastosphere*, the wall of which, composed of a single layer of blastomeres, is the *blastoderm*.

The blastomeres of the blastoderm next undergo differentiation into two kinds, distinguished by their internal activities, if not by their outward form. Of these the one set constitute the *epiblast*, the others the *hypoblast*. The further changes of the embryo are the consequences of the tendencies towards further modification resident in the epiblastic and hypoblastic blastomeres respectively. Each of these is, as it were, a germ, whence certain parts of the adult organism will be evolved.

Every series of the *Invertebrata* has now yielded a number of examples of the further modification of the blastosphere by the process of *invagination*, or *emboly*, the result of which is that the hypoblast becomes more or less completely enclosed within the epiblast. The invagination is accompanied by the diminution, or even abolition, of the blastocœle, and the formation of a cavity enclosed within the hypoblast, which is the *archenteron* or primitive alimentary cavity. The opening left by the approximated edges of the epiblast, when the process of invagination is completed, and by which the archenteron communicates with the exterior, is the blastopore. In this state the embryo is a *gastrula*.

It very commonly happens that the process of development is modified by an inequality in the size of the blastomeres; which inequality may be manifest from the bisection of the ovum, or may appear later. In this case, it usually happens that the smaller and more rapidly dividing blastomeres belong to the epiblast, and the larger and more slowly dividing to the hypoblast. Moreover, no blastocœle may arise, and the process of inclusion of the hypoblast within the epiblast may have the appearance of the growth of the latter over the former, or what is termed *epiboly*; while the archenteron may not be formed within the hypoblast till very late.

When, in cases of epiboly, the blastoderm is small in relation to the vitellus, the epiblast and hypoblast, at their first appearance, necessarily adapt themselves to the surface of the yelk; and thus the gastrula, instead of having the form of a deep cup, becomes more or less flattened and discoidal.

I am inclined to believe that all the various processes by which the gastrula or its equivalent are produced, are reducible to epiboly and emboly. Even when the epiblast and the hypoblast appear to be formed by *delamination*, or the splitting into two layers of cells of a primitively single-layered blastoderm, there seems little doubt that what happens is, either the very early inclusion of the hypoblastic blastomeres within those which give rise to the epiblast; or a very late and inconspicuous ingrowth, or invagination, of the hypoblastic region of the blastoderm.

If we employ the term gastrula in the broad sense defined above, it may be truly said that every metazoon passes through the gastrula stage in the course of its development. The question whether the mode of development of the gastrula by emboly is primitive, and that by epiboly secondary; or whether epiboly is primary and emboly secondary; or whether the two processes have originated independently, is of secondary importance, and belongs to the debateable ground of phylogeny.*

* Compare Haeckel, "Studien zur Gastræa-theorie," in his 'Biologische Studien,' 1877.

The meaning of the differentiation of the aggregate of cytodes, of which the body of a simple metazoon is composed, into a hypoblastic, or endodermal, and an epiblastic, or ectodermal group is to be sought in the physiological division of labour, which is the primary source of morphological changes. It is a separation of the aggregate of morphological units into one set with a specially nutritive, and another set, with a specially motor and protective, function. It is quite possible to conceive of an adult metazoön having the structure of a sponge embryo; moving by its ectodermal hemisphere, and feeding by its endodermal hemisphere.

The next advance in organisation of such a metazoon would doubtless consist in the more complete extension of the protective layer over the nutritive layer, with due provision for the access of the surrounding medium to the latter. It is obvious that this advance might be effected in either of two ways; the one by emboly, the other by epiboly. In the former, the blastopore would be left as the aperture of communication of the endoderm with the exterior; and the result would be the formation of an *archæostomatous* gastrula, such as that which is supposed by Haeckel to be the primitive form of the metazoon. In the latter, the blastopore would completely close up, and a new aperture or apertures must be formed in the ectoderm to subserve the ingestion of nutriment. The resulting organism would be a *deuterostomatous* gastrula.

Undoubtedly it seems natural to suppose that the first process preceded the second, in order of evolution; but the proof that it did so is at present wanting. And, however this may be, the progress of inquiry seems to throw more and more doubt upon many cases of the supposed persistence of the blastopore as the mouth. It is certain that, in the great majority of invertebrated animals, the blastopore either becomes the anus or closes up; and renewed observations are needed to determine the limits within which the archæostomatous condition prevails.

The blastocœle of the gastrula may be obliterated by the

approximation of the epiblast and the hypoblast, or it may persist and constitute the *peri-enteron,* or primitive perivisceral cavity.

Those animals which, in their adult condition, most nearly represent simple gastrulæ with obliterated blastocœle, are the *Physemaria* and *Hydra;* cup-shaped bodies with an oval opening at one end, the walls of which are made up simply of an ectoderm and an endoderm.*

In the great majority of the *Metazoa,* a further advance in complication is effected by the appearance, between the epiblast and the hypoblast, of cytodes, either isolatedly or in a continuous layer, which constitute the mesoblast, and eventually are converted into mesodermal structures. The origin of these is still a matter of doubt, but in many cases it appears to be unquestionable that they are derived from the hypoblast.

The perienteron, more or less interrupted and broken up by the constituents of the mesoblast, may give rise directly to the perivisceral space, or channels, of the adult, which thus constitute a *schizocœle.* It is hardly doubtful, I think, that the perivisceral cavity takes its origin in this manner in the *Rotifera,* the entoproctous *Polyzoa,* the Echinopædia of the Echinoderms, the *Tunicata,* and the *Nematoidea.*

On the other hand, in many *Invertebrata,* one or more diverticula of the archenteron extend into the perienteron and its contained mesoblast. Sometimes, as in the *Cœlenterata,* these remain connected with the alimentary cavity throughout life, and are termed gastrovascular canals. In other cases (*Echinodermata, Brachiopoda, Chætognatha*) they become shut off; their cavities constitute a variously modified *enterocœle;* and their walls give rise, along with the primitive mesoblastic elements, to the mesoderm.

To which of these two possible sources of the mesoderm, the mesodermal structures of the *Annelida* and the *Arthropoda,* which so very generally take on the form of two

* I do not think that Kleinenberg's fibres in *Hydra* strictly represent a mesoderm, though they occupy the position of one.

longitudinal germ-bands in the embryo, and subsequently undergo segmentation, are to be referred, is a very interesting, but, as yet, unsolved problem. It is possible that they are solid representatives of the hollow diverticula which, in other animals, give rise to the enterocœle; in which case, the perivisceral cavity in these animals will be a virtual enterocœle. On the other hand, they may merely represent the cells of the mesoblast of the entoproctous *Polyzoa* and of the Echinopædia. and their perivisceral cavity would then be a schizocœle. But it is needless to pursue this topic further; enough has been said to show conclusively that, however different one invertebrated animal may be from another, the study of development proves that each, when traced back through its embryonic states, approaches the earlier stages of all the rest; or in other words, that all start from a common morphological type, and even in their extremest divergence retain traces of their primitive unity.

It is very important to remark that these morphological generalisations, so far as they are correctly made, are simple statements of fact, and have nothing to do with any speculations respecting the manner in which the invertebrated animals with which we are acquainted have come into existence. They will remain true, so far as they are true at all, even if it should be proved that every animal species has come into existence by itself and without reference to any other. On the other hand, if there are independent grounds for a belief in evolution, the facts of morphology not only present no difficulty in the way of the hypothesis of the evolution of the *Invertebrata* from a common origin, but readily adapt themselves to it.

Hence the numerous phylogenic hypotheses which have of late come into existence, and of which it may be said that all are valuable, so far as they suggest new lines of investigation, and that few have any other significance. do not desire to add to the number of these hypotheses; and I will only venture to remark that, in the absence of any adequate palæontological history of the *Invertebrata*,

any attempt to construct their Phylogeny must be mere speculation.

But the oldest portion of the geological record does not furnish a single example of a fossil which we have any reasonable grounds for supposing to be the representative of the earliest form of any one of the series of invertebrated animals; nor any means of checking our imaginations of what may have been, by evidence of what has been, the early history of invertebrate life on the globe.

Already, indications are not wanting that the vast multitude of fossil Arthropods, Mollusks, Echinoderms, and Zoophytes now known will yield satisfactory evidence of the filiation of successive forms, when the investigations of palæontologists are not merely actuated by the desire to discover geological time-marks and to multiply species, but are guided by that perception of the importance of morphological facts which can only be conferred by a large and thorough acquaintance with anatomy and embryology. But, under this aspect, the palæontology of the *Invertebrata* has yet to be created.

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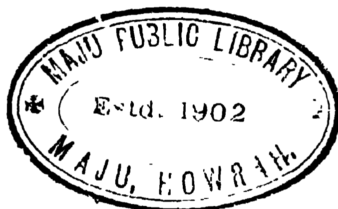
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